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EOCENE RODENTS, PRUETT FORMATION, SOUTHWEST TEXAS; THEIR PERTINENCE TO THE ORIGIN OF THE SOUTH AMERICAN CAVIOMORPHA

by

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Eocene Rodents, Pruett Formation, Southwest Texas; their Pertinence to the Origin of the South American Caviomorpha[1]

By Albert E. Wood[2]

ABSTRACT

The rodents from three localities in the Pruett Formation of the Buck Hill Volcanic Group from the Big Bend region of Texas are described. Included are the paramyids *Thisbemys plicatus*, *Microparamys minutus*, *Lophiparamys* sp. indet., and at least one indeterminate paramyid; a new species, *M. boskeyi*, of the cylindrodont genus *Mysops*; and a hystricognathous rodent of uncertain familial position, *Prolapsus*, new genus. *Prolapsus* is represented by *P. sibilatoris*, new species; *P. junctionis*, new species; and a third, smaller but indeterminate species. The rodents both individually and collectively strongly support a Middle Eocene (Bridgeran) age for the lower part of the Pruett Formation. *Prolapsus* is the first fully hystricognathous rodent to be reported from the Eocene of any part of the world. It is already too advanced in the characters of the cheek teeth to have been ancestral to the South American Caviomorpha. The incisor enamel is of the pauciserial type, characteristic of the primitive Eocene rodents, the families Paramyidae and Sciuravidae, and the mid-Eocene cylindrodont *Mysops*. Although the incisor enamel and the cheek teeth show that *Prolapsus* could not have been a caviomorph, it seems probable that the Caviomorpha were derived from Middle American Eocene ancestors of the same general stock as *Prolapsus*. The presence of *Prolapsus* in North America is a weighty argument against late Eocene trans-Atlantic migration of rodents. Unknown but probably related forms, from southwest Asia, were presumably ancestral to the African Phiomorpha.

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INTRODUCTION

During the summer of 1971, field parties from The University of Texas at Austin discovered fossil mammalian assemblages, including rodents, at three localities in the Agua Fria Quadrangle, Brewster County, southwest Texas.[3] One of these, TMM locality 41372, the source of the Whistler Squat local fauna, has produced the largest number of individual rodents (97) and one of the two rodent specimens from this area that include two or more teeth associated in a jaw. The Whistler Squat local fauna comes from a very restricted zone in the Pruett Formation of the Buck Hill Volcanic Group. The fossils were limited to about three feet of sediments immediately above a six-inch ignimbrite, about 50 feet above the base of the Tertiary sequence in this region. The other rodents come from TMM localities 41443 and 41444, about 0.6 mile apart and in the basal conglomerate of the Pruett Formation. Six rodent specimens (one a lower jaw) from locality 41443, and 15 from locality 41444, are included in the present study.

One of the two jaws, described below as the holotype of *Prolapsus sibilatoris*, new genus, new species, is particularly interesting and important in the overall picture of rodent evolution, as it is the first specimen to have been recognized as a fully hystricognathous rodent in the earlier Tertiary of North America, and the first specimen to have been so recognized from the Eocene of the entire world (Wood, 1972). Since this discovery, certain other North American Eocene fossils have been independently determined to be hystricomorphous but perhaps not hystricognathous (Wahlert, in press), and Black and Stephens (1973) have described an Eocene hystricognathous genus from Mexico. In addition to the great importance of the *Prolapsus* jaw in attempts to unravel major questions of rodent phylogeny, the rodents as a whole point unmistakably to a middle Eocene (Bridgeran) age for the faunule as a whole, and are therefore an important factor in establishing the age of these beds.

Since the specimens discussed in this paper are all in the collections of the Texas Memorial Museum of The University of Texas at Austin, and since the locality numbers are those of the same institution, the abbreviation TMM (Texas Memorial Musem) has usually been omitted. Specimen numbers without prefixes belong to the Texas Memorial Museum; numbers preceded by a hyphen are abbreviated and include the last preceding five digit locality number, e.g., 41372-1, -2. Other abbreviations used are: OR—observed range; $\bar{X}$—mean; s—standard deviation; and V—coefficient of variation.

The classification of rodents used is that of Wood (1965a). For reasons that I discuss elsewhere (Wood, in press 2), I do not feel that the union of the Paramyidae

[3]Detailed descriptions of the localities are on file at the Vertebrate Paleontology Laboratory, Texas Memorial Museum, The University of Texas at Austin.

and Ischyromyidae proposed by Black (1968) is justified. Furthermore, the arrangement of the paramyids within that family as given by Wood (1962) seems vastly preferable to the shifts proposed by Black (1971), which ignore all features of the animals except the cheek tooth patterns.

I am deeply grateful to Professor J. A. Wilson of The University of Texas at Austin, who has allowed me to study this most interesting collection of fossils, and who had thin sections of the incisors of *Prolapsus sibilatoris* prepared for me. The preparation of this paper was assisted by Grant No. 150 from the Marsh Fund of the National Academy of Sciences. Mr. and Mrs. L. M. Boskey provided vital assistance in connection with the statistical portions of the manuscript. The field studies that produced the fossils were supported by the Geology Foundation, The University of Texas at Austin. Mr. and Mrs. Billie Pat McKinney, the lessees, Messrs. J. H. Burton, Sid Burton, and Macon Richmond, owners of the Agua Fria Ranch, provided invaluable assistance to the field parties that made these collections.

SYSTEMATICS

Family PARAMYIDAE Miller and Gidley, 1918
Subfamily PARAMYINAE Simpson, 1945
Thisbemys plicatus Wood, 1962
(Figs. 1, 2A)

A lower jaw with M_{1-2} and the incisor (41443-26) and 24 isolated teeth (19 from locality 41372, two from locality 41443, and three from locality 41444) are referred to this species (tables 1-2). As pointed out by Wood (1962, p. 111-112), this species, from the lower Bridger, grades insensibly into the more advanced *Thisbemys corrugatus* from the upper Bridger, and the two can be separated, in collections from near the dividing line, only statistically.

The corrugation of the cheek teeth of the Texan fossils is relatively fine, the ridgelets not having dentinal cores, so that they were eliminated after wear (fig. 1 F, H, K and M). The differences between the two teeth shown in fig. 1 J and K, for example, are almost entirely due to wear. Because of the relatively small size of the corrugations and the fact that they are eliminated by wear without producing anticlinal dentine valleys along their axes, these teeth are closer to those of *T. plicatus* from the early Bridgeran Blacks Fork than to the more heavily ridged teeth of *T. corrugatus* from the Twin Buttes. Most dental measurements (tables 1-2) fall within the OR of both Bridgeran species, but 14 fall outside the previously known range for *T. plicatus* (8 larger and 6 smaller), and 9 fall beyond that of *T. corrugatus* (8 smaller and one larger). However, when these measurements are converted into deviations in terms of the s of the Bridger populations, only one measurement (anteroposterior diameter of 41372-131) is more than 3.0 s from the mean of *T. plicatus* (3.1 s larger), and two measurements (one larger, one smaller) are 3.0 s from the mean. Six measurements, however, are 3.0 s or more smaller than the means of *T. corrugatus,* of which three are considerably over 3.0 (width hypolophid, 41372-274, -3.3 s; width metalophid, same specimen, -3.6 s; and transverse diameter, I_1, 41443-26, -3.5 s. Thus, the measurements agree with the crown pattern, in indicating that these specimens are closer to *T. plicatus* than to *T. corrugatus*. The lower incisor (fig. 1 P) is unusually narrow, for either species, and has a faint sulcus on its anterior face, not seen in any of the Wyoming specimens. The

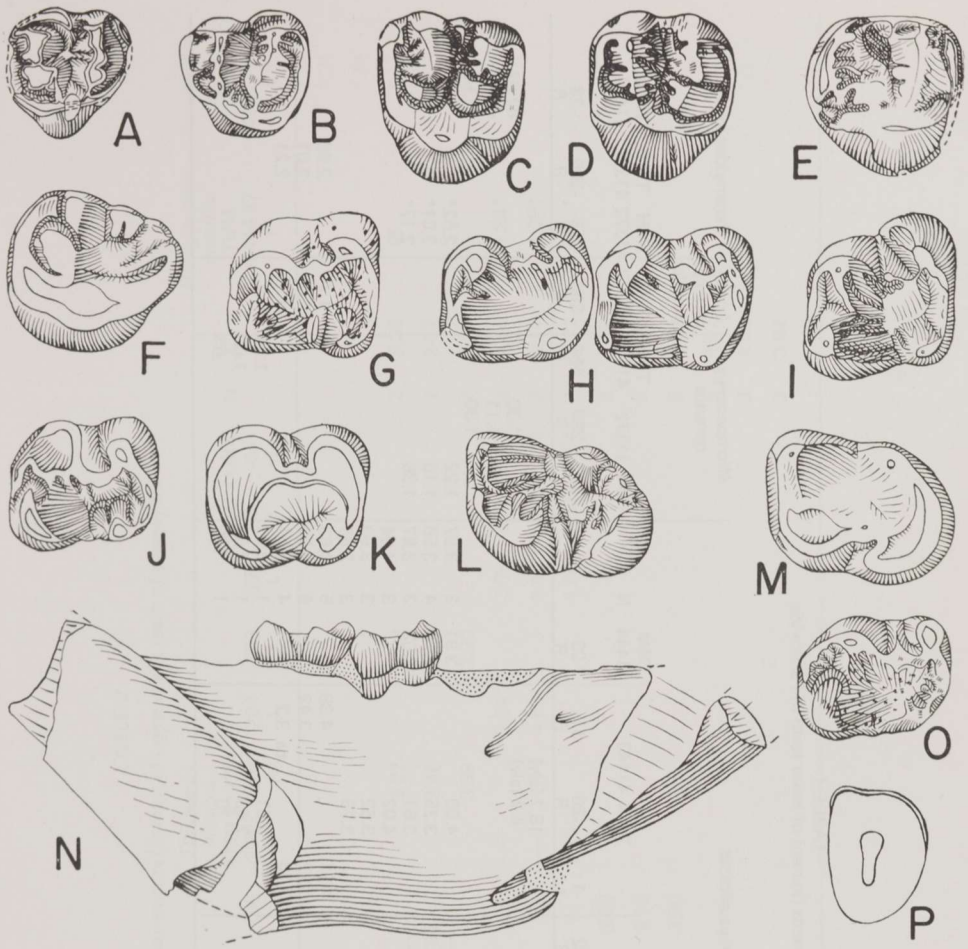

Fig. 1. Teeth and jaw of *Thisbemys plicatus*. Teeth X 5, jaw X 3.

A. RdP^4, 41372-270, anterior end to the right. B. LdP^4, -296. C. LM^2, -135. D. LM^2, -122. E. RM^3, -56, anterior end to the right; all enamel broken off protocone. F. LM^3, -129. G. RM_1, -25, H. RM_{1-2}, 41443-26. I. RM_2, 41444-23. J. RM_2, 41372-133, K. RM_2, -131. L. LM_3, -130. M. LM_3, 41443-1. N. Lateral view, right lower jaw, -26. O. RM_3, 41372-274. P. Cross section of RI_1, from the front, 41443-26.

shape of the pulp cavity is more like that of *T. plicatus* than like that of *T. corrugatus* (Wood, 1962, p. 111).

The lower jaw (fig. 1 N) agrees with the jaws of both the Bridger species in the presence of two mental foramina and in having a straight and slightly everted diastemal margin.

The upper deciduous premolar of *T. plicatus* has not previously been illustrated, so the two teeth from locality 41372 (-270 and -296) deserve description (fig. 1 A, B). The anterior and posterior cingula are large, the latter being nearly or quite continuous into a buccal cingulum. The protoloph is multicuspidate, and reaches the anterior side of the protocone. The metaloph, with a large metaconule, joins the posterior end of the protocone, behind which the posterior cingulum is enlarged to form a prominent hypocone, which extends appreciably linguad of the protocone.

TABLE 1
Measurements (in mm) of lower teeth of Paramyids

	Thisbemys plicatus												*Microparamys minutus*			*Lophiparamys* sp. indet.	Paramyidae indet.		
	TMM 41372							TMM 41443			TMM 41444	N	$\bar{X}$	TMM 41372		TMM 41444	TMM 41372	TMM 41372	TMM 41372	TMM 41444
	-25 R	-117 L	-130 L	-131 R	-133 R	-274 R	-302 R	-1 L	-26 R	-31 R	-23 R			-260 L	-298 R	-56A L	-286 L	-259 R	-305 R	-28 R
P_4–M_3									18.7 (alv)											
P_4 anteroposterior									4.3 (alv)						1.36					d2.02
width, metalophid															1.11					d1.34
width, hypolophid															1.30					d1.58
M_1 anteroposterior	4.00						---		4.00		3.91	3	3.97	1.22				2.52*		
width, metalophid	3.63						3.64		3.25		3.71	4	3.56	1.16				2.01*		
width, hypolophid	3.97						---		3.61		4.02	3	3.87	1.36				2.17*		
M_2 anteroposterior				4.21	3.88				4.02			3	4.04							
width, metalophid				3.79	3.35				3.62			3	3.59							
width, hypolophid				3.76	3.37				3.75			3	3.63							
M_3 anteroposterior		4.93	4.88			4.03		4.91		4.38		5	4.63				1.26		2.68	
width, metalophid		3.89	3.65			3.26		3.72		3.42		5	3.59				1.18		2.01	
width, hypolophid		3.82	3.42			3.05		3.76		ca. 3.2		4	3.51				1.10		2.21	
I_1 anteroposterior									3.61			1	3.61			1.88				
transverse									2.63			1	2.63			1.00				
ratio									.70			1	.70			.53				

* = M_1 or M_2
d = deciduous

TABLE 2

Measurements (in mm) of upper cheek teeth of paramyids

	Thisbemys plicatus TMM 41372															*Microparamys minutus* TMM	Paramyidae indet. TMM
	-56 R	-122 L	-129 L	-132 L	-134 R	-135 L	-136 L	-254 R	-270 R	-294 L	-296 L	-309 L	-63 R	-64 L	N	$\bar{X}$	41444-27 R	41372-271 L
P^3 anteroposterior																		1.3+
transverse																		1.5+
dP^4 anteroposterior									3.22		3.38				2	3.30		
width, protoloph									3.48		3.06				2	3.27		
width, metaloph									3.39		3.20				2	3.30		
M^1 anteroposterior								——		3.64*		3.65	3.63	3.63	3	3.64	1.24*	
width, protoloph								——		4.59*		4 40	4.02	3.99	3	4.14	1.39*	
width, metaloph								3.83*		——		4.20	3.49	3.51	3	3.73	1.23*	
M^2 anteroposterior		3.86				3.88	3.63								3	3.79		
width, protoloph		4.35				4.41	4.12								3	4.29		
width, metaloph		4.31				4.00	3.96								3	4.09		
M^3 anteroposterior	4.07		4.60	4.23	3.92										4	4.21		
width, protoloph	4.22		4.15	——	3.75										3	4.04		
width, metaloph	3.90		4.13	——	3.69										3	3.91		

*M^1 or M^2

All of these features represent advances over the more primitive dP^4 of *Paramys delicatus* (Wood, 1962, fig. 9 E). There is a minute anterior wear facet on one specimen (-296), indicating that there had been a tooth in front of dP^4, either dP^3 or P^3, although it is impossible to determine which (Wood, 1969, p. 608).

Isolated specimens of M_1 or M_2 were separated on the basis that, on M_2, the widths of the metalophid and hypolophid are nearly equal, whereas on M_1, the width of the metalophid is considerably smaller (fig. 1 H and table 1, 41443-26), as is also true of the Bridger material (Wood, 1962, table 41). There was somewhat more uncertainty in separating M^1 and M^2, but the two transverse widths of M^2 are generally more nearly equal than are those of M^1, due to the greater development of the hypocone in the former tooth.

The unworn M_3 (fig. 2A) clearly shows the great complexity of this tooth, the posterior slopes of the trigonid and the entire talonid basin being covered with irregular ridges that mask the basic pattern of the tooth. This specimen was drawn at a higher magnification than the teeth on fig. 1, to show the complex ridges. With wear, these minor ridges become eliminated, but at an intermediate stage of wear (fig. 1 O) the talonid basin is covered with small pock marks, the last remnants of the valleys between the original rugosities. There is a very deep lingual gorge in front of the entoconid (figs. 1 L, 2 A), that continues to be recognizable even after extensive wear (fig. 1 M, O). The lateral crest of the hypoconid reaches the buccal margin of the tooth (figs. 1 L, 2 A). At an intermediate stage of wear, this crest bears a wear surface that reaches the edge of the tooth (fig. 1 O).

No differences were noted between the teeth of the earlier populations from localities 41443 and 41444 (the basal conglomerate) and those from the Whistler Squat local fauna.

Subfamily MICROPARAMYINAE Wood, 1962

Microparamys minutus (Wilson), 1937

Fig. 2 B-E

Two lower teeth from locality 41372 (-260, LM_1 and -298, RP_4) and one upper molar from locality 41444 (-27, RM^1 or ^{2}) are referred to this species. The two molars are smaller and the lower premolar is larger (tables 1-2) than any specimens in the small sample from the Bridger Formation (Wood, 1962, table 54), but the material from the Powder Wash described by Dawson (1968, p. 335-340, table 3) and referred to *M. minutus*, extends the size range of that species to include the present specimens. Crenulations do not show on either lower tooth, apparently having been removed by wear.

The premolar (fig. 2 B) has the high metaconid and small protoconid characteristic of the species, and the posterior arm of the protoconid curves forward into the rear of the metaconid (cf. Wood, 1962, fig. 54 B). The entoconid is separated from the posterolophid as in the specimens from Wyoming, but in contrast to the Powder Wash material (Dawson, 1968, fig. 12). A very faint swelling extends into the talonid basin from the entoconid.

The lower molar (fig. 2 C) is very similar to those figured by Wood (1962, fig. 54 D) and Dawson (1968, figs. 13-15), showing the characteristic valley between the anterolophid and the protoconid, and the delayed connection of the entoconid and posterolophid. The protoconid and metaconid are connected by a crest, coming

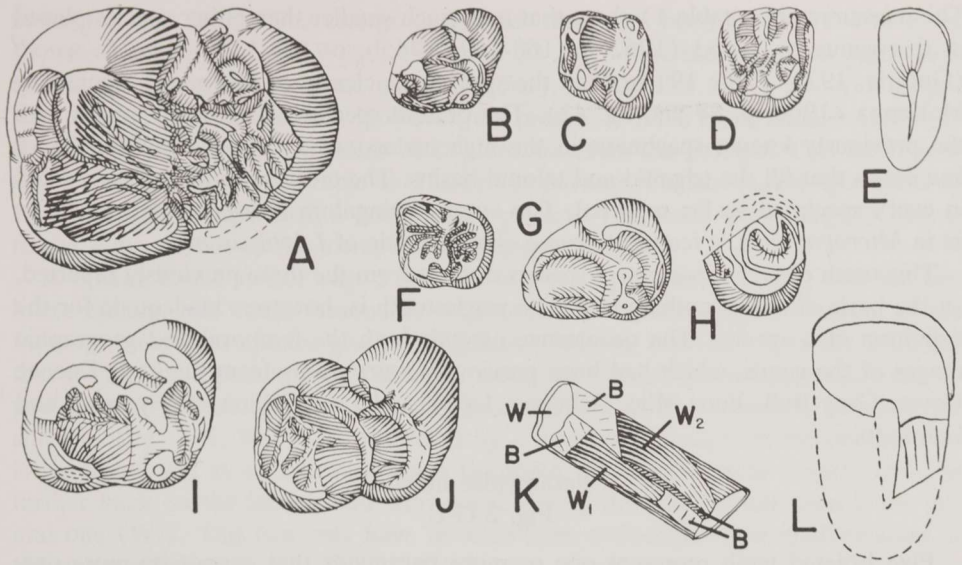

Fig. 2. Teeth of paramyids, X 10.

A. *Thisbemys plicatus*, RM_3, 41443-31. B. *Microparamys minutus*, RP_4, 41372-298. C. *M. minutus*, LM_1, -260. D. *M. minutus*, RM^1 or ^{2}, 41444-27, anterior end to the right. E. *M. minutus*, LI_1, -56A, cross section seen from rear. F. *Lophiparamys* sp., LM_3, 41372-286. G. Paramyid indet., RdP_4, 41444-28. H. Paramyid indet., LP^3, 41372-271. I. Paramyid indet., RM_1 or $_2$, -259. J. Paramyid indet., RM_3, -305. K-L, Paramyid indet., LI_1, -243A. K. posterior surface showing distal wear surface (W), two non-coplanar posterior wear surfaces (W_1, W_2) and broken areas (B). L. Cross section of tooth from rear.

from near the center of the protoconid, that completely closes the trigonid basin, as in some of the Powder Wash material (Dawson, 1968, fig. 15). The mesostylid is very small and indistinctly separated from the metaconid, again as in some of the Powder Wash specimens.

The upper molar (fig. 2 D) is very similar to those previously described for *M. minutus* (Wood, 1962, fig. 54 E; Dawson, 1968, fig. 9). The anterior cingulum is continuous and is separated from the protoloph at both ends. The hypocone, of cingular origin, is continuous with the posterior cingulum. The protoloph, apparently composed of several cusps, runs to the anterior end, and the complex metaloph unites with the posterior end, of the protocone. The chief difference in pattern between this tooth and the previously described teeth of *M. minutus* is that the mesostyle is transversely elongate in the Texas specimen.

An isolated left lower incisor, 41444-56A, is perhaps referable to this species (fig. 2 E). It certainly does not fit into any other taxon recognizable in the faunules.

The specimens are close to the teeth of the Bridger sample of *M. minutus*, both in size and in morphology, and agree in almost all details with the teeth from Powder Wash referred to this species by Dawson. There is no present basis for separating the Texas animals from *M. minutus*.

Lophiparamys sp. indet.
Fig. 2 F.

An isolated LM3, 41372-286, can best be referred to this poorly known genus.

The measurements (table 1) show that it is much smaller than either species placed in this genus by Wood (1962, p. 168-169; 1965b, p. 125-127), than *L. woodi* (Guthrie, 1971, Table 19) or than the specimens, clearly of this genus, figured by McKenna (1960, p. 84 and fig. 42). The present specimen (fig. 2 F) agrees with the previously known specimens in the high metaconid and in the multiplicity of low crests that fill the trigonid and talonid basins. The crests seem to differ in detail in every specimen so far reported. The anterior cingulum swings around buccally, as in *Microparamys*, a feature likewise characteristic of *Lophiparamys*.

This tooth clearly represents a species distinct from the three previously reported, on the basis of size if nothing else. The single tooth is, however, inadequate for the definition of a species. The occurrence extends both the temporal and geographic ranges of the genus, which had been previously known only from the early Eocene (lower Gray Bull, Four Mile, Debeque, Lysite and Lost Cabin) of Wyoming and Colorado.

Paramyidae indet.
Fig. 2 G-L

Five isolated teeth represent one or more paramyids that cannot be more precisely identified at the present time.

Two lower molars (41372-259, RM_1 or $_2$ and -305, RM_3) are conspecific. They agree in having a high metaconid, from which four crests (the anterior cingulum and three from the metaconid itself) extend toward the protoconid, which also sends multiple crests toward the metaconid (fig. 2 I-J). The distinctness of these crests is reduced with wear. The entoconid is continued by a swelling toward the mesoconid, and there may be a complete hypolophid (fig. 2 J). There are accessory hypoconulids on both teeth, that show up more clearly after wear. These two teeth are most similar in size (table 1) and in general pattern to teeth of some of the smaller species of *Paramys*, belonging to the *P. excavatus* species group, but are more advanced in the deveolpment of the hypolophid. They are closest, morphologically, to *P. huerfanensis* of the middle Eocene of southeastern Colorado, one of the species whose known occurrence is nearest to the Big Bend area. They are, however, distinctly larger and more advanced than are the teeth of *P. huerfanensis*.

A peculiar lower premolar (41444-28, fig. 2 G) is almost identical, both in size (table 1) and pattern, with an unidentified paramyid from the middle Eocene Green River Formation (Wood, 1962, p. 241, fig. 89 B). The metaconid is very high, and seems to be as much an elongate crescent as a cusp. Except for an opening at the middle of the lingual margin of the tooth, there is an almost continuous marginal crest, with the protoconid, hypoconid, hypoconulid and entoconid being merely slight enlargements of the crest. The hypolophid curves forward from the entoconid into the posterior arm of the protoconid, enlarging in the middle of the talonid basin into what might be called an entoconulid (fig. 2 G). A prominent feature of the tooth is the major backward swelling of the metaconid, that has filled most of the anterior part of the talonid basin. There are similarities between this tooth and the one figured as dP_4 of *Microparamys minutus* by Dawson (1968, fig. 18), but there are differences in detail, and the Texas specimen is nearly twice as large. It is possible that this tooth is dP_4 of the same species as the two lower molars discussed above.

A broken LP^3 (41372-271) is unusually complicated for a middle Eocene

paramyid (fig. 2 H). The closest similarities that have been noted are with P^3 of *Leptotomus bridgerensis* (Wood, 1962, fig. 33 A), where there are two partly separated buccal cusps (paracone and metacone), an anterior and a posterior cingulum, and a lingual protocone. However, the present tooth is much smaller (table 2) than P^3 of any known specimens of *Leptotomus* from the Bridger. This tooth is of the correct size to be referable to *Thisbemys plicatus*, but no known specimens of P^3 of that genus have such a complicated pattern. The tooth is too large to belong to the same species as the lower molars discussed above.

A broken lower incisor (fig. 2 K-L) is of the proper size to belong with the two lower molars, and could reasonably be interpreted as belonging to a rodent of the *Paramys excavatus* species group. Its greatest interest, however, is in the evidence that it gives of malocclusion. The tip is worn flat (possibly but improbably due to post-mortem abrasion). The diagonal wear surface on the dentine is actually two surfaces (fig. 2 K, W_1, W_2), separated by a longitudinal scarp in the dentine that is not continued as a fracture through the tooth. The medial wear surface (W_2) is farther back on the incisor and worn more deeply into the dentine than is the lateral one (W_1). This can only have resulted from malocclusion or malformation of the upper incisors.

Family CYLINDRODONTIDAE Miller and Gidley, 1918

Mysops Leidy, 1871

Genotype.—*M. minimus* Leidy, 1871.

Referred species.—*M. parvus* (Marsh), 1872; *M. fraternus* Leidy, 1873; *M. boskeyi,* new species.

Revised diagnosis.—Cheek teeth P^2_1, M^3_3; teeth brachydont with cross crests more highly developed than in *Sciuravus*; early stages of lingual hypsodonty in upper teeth, no to slight hypoconid hypsodonty in lowers; incisors more slender and less vertically implanted than in later cylindrodonts; mandible slender; protoloph and metaloph convergent toward protocone, never toward hypocone; metaloph poorly developed; connection between metaconule and protocone weak or absent, and progressively replaced by metaconule-posteroloph union; metaconule only slightly distinct from metaloph, protoconule rarely separable from protoloph; hypocone merely an enlargement of posterior cingulum, most distinct on M^{1-2}, and progressively separated from protocone by lingual groove; protostyle on anterior cingulum often nearly as large as hypocone; trigonids of lower cheek teeth high, usually twice or more the height of talonid; buccal cusps marginal; metalophid runs from posterior arm of protoconid to middle of rear, or even to buccal side, of metaconid; axis of trigonid basin diagonal; hypolophid of molars complete, often showing an entoconulid at its middle; hypolophid of premolar variably complete; ectolophid strong and linear, with no mesoconid; posterolophid elevated, with strong hypoconulid obvious after wear; lower molars 2 or 3-rooted; lower incisors with flattened anterior faces (modified after Wilson, 1938, p. 207-208).

Distribution.—Blacks Fork and Twin Buttes members, Bridger Formation of Wyoming; Pruett Formation of Big Bend region of Texas; and possibly upper Washakie of southern Wyoming.

Mysops, as pointed out by Wilson (1949, p. 94), is clearly the only known middle Eocene representative of the Cylindrodontidae. Except for a citation of

Mysops? from the upper Washakie (Black and Dawson, 1966, table 1, p. 335), I know of no material later than middle Eocene that is referable to *Mysops*. Most of the diagnostic features of the Cylindrodontidae are either not present in *Mysops* (the heavy, vertically erupting incisors, the stocky lower jaws, and the peneplaned surface of the crests of the lower cheek teeth); are not preserved in any so-far described specimens of *Mysops* (the characteristic skull features); or are merely incipiently developed (the unilateral hypsodonty of the upper cheek teeth, the hypoconid hypsodonty of the lowers, and the strong union of the metaconule with the posteroloph). On the other hand, although clearly anticipating the later cylindrodonts and therefore referable to that family, *Mysops* is not widely separable, in its cheek tooth characteristics, from its contemporaries that are included in the Sciuravidae. Wahlert, however, suggests that the cyindrodonts and ischyromyids have so many features of their cranial foramina in common, features that they do not share with either the Paramyidae or the Sciuravidae, that they must have had a rather distinctive common ancestor. He would derive this ancestor ultimately from the Paramyidae rather than from the Sciuravidae (1972, p. 212).

The specimens in the Yale Peabody Museum, referred to *Mysops parvus* by Wilson (1938, p. 210-212), are sufficiently numerous to permit a population analysis to be made (table 3). Throughout the measurements of this population, V is larger than in most Eocene rodent populations, due in part to the fact that the collection is a mixture of specimens from both members of the Bridger Formation, but also

TABLE 3

Measurements (in mm) of teeth of *Mysops parvus* in the Yale Peabody Museum

	Lower Teeth				Upper Teeth		
	N	OR	$\bar{X}$ s	V	N	OR	$\bar{X}$
P_4–M_3 alveolar	19	5.90–7.03	6.49±.26	4.01			
crown	12	5.80–6.80	6.24±.29	4.65			
P4 anteroposterior	23	1.08–1.53	1.35±.11	8.15	5	1.22–1.37	1.30
width, anterior	22	0.91–1.20	1.07±.08	7.48	5	1.32–1.58	1.48
width, posterior	25	1.06–1.41	1.26±.09	7.14	5	1.41–1.63	1.57
M1 anteroposterior	37	1.21–1.82	1.54±.13	8.44	4	1.33–1.45	1.41
width, anterior	31	1.20–1.48	1.32±.07	5.30	4	1.49–2.09	1.89
width, posterior	34	1.30–1.58	1.45±.08	5.52	4	1.73–2.06	1.91
M2 anteroposterior	40	1.42–1.94	1.63±.10	6.13	4	1.43–1.90	1.59
width, anterior	37	1.37–1.61	1.50±.06	4.00	4	1.86–2.12	1.95
width, posterior	40	1.41–1.75	1.56±.08	5.13	4	1.71–2.03	1.85
M3 anteroposterior	27	1.56–2.07	1.78±.08	4.49	2	1.41–1.48	1.45
width, anterior	26	1.34–1.66	1.48±.09	6.08	2	1.62–1.92	1.77
width, posterior	27	1.29–1.72	1.45±.11	7.59	2	1.55–1.84	1.70
I_1 anteroposterior	32	1.46–2.40	1.90±.19	10.00			
transverse	32	1.08–1.80	1.30±.13	10.00			
ratio	32	.59– .79	.69±.05	7.25			

supporting Wilson's suggestion (1938, p. 214) that more than one species may be included. The large size of V for the incisors is due to the continual growth that occurs in these teeth, a probability supported by the fact that the ratio of the incisor diameters is less variable than are the measurements themselves (table 3).

Mysops was, presumably, ancestral to *Pareumys* (Wilson, 1940a, p. 107) and, through it, to the Chihuahua *Jaywilsonomys* (Ferrusquia and Wood, 1969, p. 6). The diversity of the known material of *Mysops* suggests that it may include a series of lineages that were also ancestral to other later cylindrodonts, such as *Cylindrodon, Pseudocylindrodon* and *Ardynomys*, but these lineages have not, as yet, been identified (Wilson, 1949, p. 94). Furthermore, as Wilson pointed out, it is still impossible to determine how many valid species are represented in the Bridger collections. Black (1970, p. 206-207) suggests that *Pseudocylindrodon tobeyi* from the late Eocene of Badwater might have been ancestral to *Cylindrodon* as well as to the Oligocene species of *Pseudocylindrodon*. He concludes that "if the Badwater species was not directly ancestral to the Oligocene cylindrodonts, it was certainly much closer to the *Mysops-Cylindrodon* lineage than was any species of *Pareumys*" (Black, 1970, p. 207). In his opinion, therefore, *Pareumys* would seem to be on a side line, similar to the position in which I place it.

Mysops boskeyi, new species[4]
Figs. 3-4

Holotype.—TMM 41372-140, isolated $R\bar{M}^1$.

Hypodigm.—Holotype, nine specimens of P^4 (one, 41372-255, too broken to measure), four of M^1, seven of M^2, five of M^3, one of P_4, six of M_1, three of M_2, six of M_3, seven of I^1, and one of I_1, as listed in tables 4 and 5.

Diagnosis.—High crowned for *Mysops*, much lower crowned than *Pareumys troxelli*; metaconules of P^4-M^2 and sometimes of M^3 more closely connected to posteroloph than to protocone, so that metaloph always unites with posteroloph first, but after more wear may also unite with protocone; protoconule weak or absent in P^4; hypocone of P^4 prominent and lingual to protocone; protostyle sometimes as large as hypocone, the latter rarely appearing distinct before wear; M^3 with or without metaconule; lower incisor with flattened anterior face, upper slightly rounded; pulp cavity of incisors comma-shaped in cross section; tooth measurements as given in tables 4-5.

Distribution.—The holotype and most referred specimens are from locality 41372, but the lower premolar is from locality 41443. Middle Eocene Pruett Formation, Big Bend region of Texas.

DESCRIPTION

The twenty-six upper cheek teeth, fifteen lowers, seven upper and one lower incisor referred to this species make it the most abundant rodent in the Whistler Squat local fauna (table 9). It is rare (one specimen) in the basal beds.

All the specimens are isolated teeth. There is, therefore, some uncertainty in the discrimination of $M^{1\text{-}2}_{1\text{-}2}$, but they have been separated on the basis of proportions.

[4]I take great pleasure in naming this species for Grace and Loeser Boskey, in appreciation for their logistical support of important parts of the preparation of this paper.

TABLE 4

Measurements (in mm) of upper teeth of *Mysops boskeyi*, n. sp.*

	Holo-type -140 R	-137 L	-138 L	-141 L	-142 L	-144 L	-147 R	-148 R	-149 L	-150 R	-179A R	-261 R	-264 L	-267 R	-276 R	-280 L	-282 R	-283 L	-287 R	-288 R	-290 L	-292 L	-303 L	-306 R	-307 R	N	OR	$\bar{X}$
P^4 anteroposterior				1.63				1.43	1.50	1.63				1.64							1.89		1.70		1.73	8	1.43-1.89	1.64
width, protoloph				1.97				1.95	2.09	2.15				2.14							2.30		2.00		1.90	8	1.90-2.30	2.06
width, metaloph				1.93				1.78	2.12	1.97				2.07							2.18		1.93		1.91	8	1.78-2.18	1.99
M^1 anteroposterior	1.76		1.59			1.82							1.83			1.93										5	1.59-1.93	1.79
width, protoloph	2.25		2.05			2.38							2.20+			2.44										4	2.05-2.44	2.28
width, metaloph	2.13		1.90			2.14							1.97+			2.30										4	1.90-2.30	2.12
M^2 anteroposterior		1.77		1.79							1.72							1.88	1.71			1.79		1.94±		7	1.71-1.94	1.80
width, protoloph		2.33		2.19+							2.22							2.01	2.14			–––		2.30±		6	2.01-2.33	2.20
width, metaloph		2.22		2.07							1.95							1.97	–––			–––		2.23±		5	1.95-2.23	2.09
M^3 anteroposterior							1.89					1.63			1.99		1.77			1.73						5	1.63-1.99	1.80
width, protoloph							2.28					1.87			2.15		1.85			–––						4	1.85-2.28	2.04
width, metaloph							1.95+					1.74			2.15		1.83			–––						4	1.74-2.15	1.92

	241 ant. R	241 post. R	241A L	241B L	241D ant. R	241D post. R	241E L	243B R	243C R	N	OR	$\bar{X}$
I^1 anteroposterior	1.81	2.18	2.12	2.17	1.28	1.46	2.30	2.07	2.34	9	1.28-2.34	1.97
transverse	1.09	1.32	1.08	1.34	0.83	0.97	1.44	1.27	1.29	9	0.83-1.44	1.18
ratio	.60	.60	.51	.61	.65	.67	.63	.61	.55	9	.51-.67	.60

*All specimens are from TMM locality 41372.

TABLE 5

Measurements (in mm) of lower teeth of *Mysops boskeyi*, n. sp.

	41372 -139 R	-145 L	-146 R	-241H R	-249 L	-250 L	-251 R	-253 L	-257 L	-258 R	268 R	-272 R	-273 L	-275 R	-277 R	-293 R	41443 -32 L	N	OR	$\bar{X}$
P_4 anteroposterior																	1.61	1	1.61	1.61
width, metalophid																	1.29	1	1.29	1.29
width, hypolophid																	1.53	1	1.53	1.53
M_1 anteroposterior		1.82	1.93		1.96				2.06					1.82		1.83		6	1.82–2.06	1.90
width, metalophid		1.44	1.50		1.68				1.88					1.68		1.44		6	1.44–1.88	1.60
width, hypolophid		1.65	1.68		1.88				1.84					1.6+		1.60		5	1.60–1.88	1.73
M_2 anteroposterior							1.90				1.75	1.86						3	1.75–1.90	1.84
width, metalophid							1.88				1.68	1.66						3	1.66–1.88	1.74
width, hypolophid							1.89				1.71	1.88						3	1.71–1.89	1.83
M_3 anteroposterior	1.95					2.03		2.24		2.08			2.42		2.16			6	1.95–2.42	2.15
width, metalophid	1.86					1.68		1.75		1.74			1.90		1.87			6	1.68–1.90	1.80
width, hypolophid	1.71					1.75		1.73		1.60			1.64		1.75			6	1.60–1.75	1.70
I_1 anteroposterior				2.17														1	2.17	2.17
transverse				1.30														1	1.30	1.30
ratio				.60														1	.60	.60

Teeth in which the protocone is far to the rear, the hypocone does not extend as far linguad as does the protocone, and the lingual valley between these cusps is very shallow, are considered to be M^1. If the hypocone is large, extends far linguad, and the lingual valley is relatively deep, the teeth are believed to be M^2. Those lower molars in which the length is considerably greater than the width are identified as M_1, since this agrees with the Yale specimens of *Mysops parvus* (table 3 and Wilson, 1938, p. 217) and with *Pareumys troxelli* (Burke, 1935, p. 12). Furthermore, the difference between the metalophid and hypolophid widths of the teeth is normally much greater on M_1 than on M_2 (tables 3 and 5). However, neither of these criteria holds universally among the Yale specimens (in place in jaws) measured for the present study (table 3), so that there may be some confusion of specimens of M_1 and M_2. The lingual hypsodonty of the upper teeth (fig. 3 G) and the hypoconid hypsodonty of the lowers (fig. 4 G) are intermediate between the conditions in *M. parvus*, where these characteristics are very slightly developed, and in *Pareumys troxelli*, where they are much more pronounced.

Nine teeth have been identified as P^4. Interdental wear facets were not certainly identified on the front of any of these teeth, which does not prove that P^3 was not present, as the contact between P^3 and P^4 in rodents is often not a tight one, and the wear facet may be difficult to identify. There is very little anterior expansion of the anterior cingulum in the parastyle region (fig. 3 A-C), which suggests that P^3 was present, as in *M. parvus*. The anterior cingulum is of variable length, and rarely (41372-290) bears a large lingual protostyle. Occasionally (-307) the parastyle is beveled by wear against the protoconid of P_4. The protoloph is complete, with little or no indication of a protoconule. At the crown surface, the hypocone is linguad of the protocone, but at the base of the crown the greatest lingual extension is formed by the protocone. The hypocone is only a slight expansion of the posteroloph until after considerable wear (fig. 3 B). The metacone is very close to the paracone (fig. 3 B-C), and sometimes the two are partially connected by a mesostyle. The metaconule is distinct and has no connection with either the protocone or the hypocone until after extreme wear, when there may be union with the protocone (-255) as well as with the posteroloph. This latter connection of the metacone is variable. If the metaloph is transverse (fig. 3 A-B), its connection with the posteroloph is usually weak to nearly nonexistent, although there is such a connection in one specimen (-150); if the metaloph is diagonal, the posteroloph connection is strong (fig. 3 C). There may be cusp-like swellings in the posteroloph, one of which generally marks the area of union with the metaconule.

The hypocone of M^1 is poorly developed, being merely a swelling on the posteroloph (fig. 3 D-F). The parastyle is prominent and the protostyle is variable, sometimes (fig. 3 E) being quite prominent and occasionally (-144) being almost as large as the hypocone. The protoconule is usually distinct but is fully united with the protoloph. Occasionally (-264) the protoconule seems to be absent. There is generally a mesostyle, but it may be minute. The metaloph is usually transverse; the metaconule is always connected firmly with the middle of the posteroloph, although it may have a subsidiary connection with the protocone (fig. 3 D). Interdental wear is initiated at the occlusal surface of the anteroloph (fig. 3 F-G).

The second molar is similar in most features to M^1. The protostyle is always smaller than the hypocone (fig. 3 H-I), the protoconule is sometimes quite indistinct, there is variation in the presence of a mesostyle, and the metaloph is always

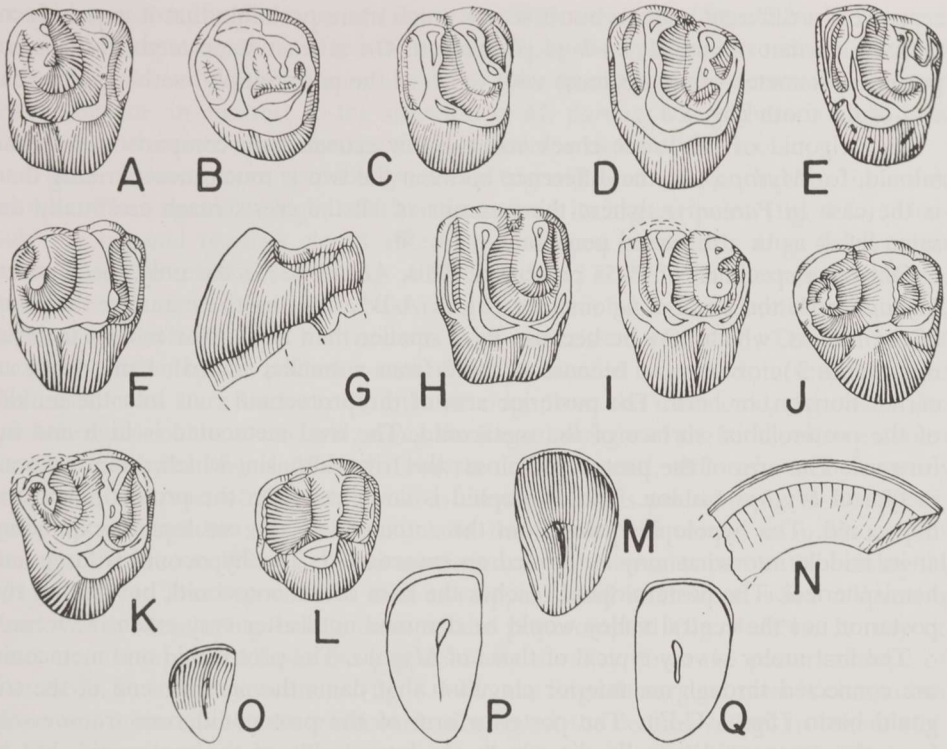

Fig. 3. Incisors and upper cheek teeth of *Mysops boskeyi*, new species, X 10 except N, which is X 5.

A. RP^4, 41372-267, anterior end to the right. B. LP^4, -303. C. LP^4, -149. D. LM^1, -144. E. LM^1, -138. F. Holotype, RM^1, -140, anterior end to the right. G. Holotype, RM^1, -140, anterior side of tooth. H. LM^2, -137. I. LM^2, -142. J. RM^3, -276, anterior end to the right. K. RM^3, -147, anterior end to the right. L. RM^3, -261, anterior end to the right, possibly *not Mysops*. M. LI^1, -241B, occlusal surface. N. LI^1, -241B, medial surface showing presumed growth lines in dentine. O. RI^1, -241D, juvenile, occlusal surface. P. RI^1, -243C, cross section from front. Q. RI^1, -241H, cross section from front.

transverse. The metaconule does not connect with the posteroloph until after considerable wear. Occasionally (fig. 3 H) there is a faint swelling running from the protocone toward the metaconule, but more often there is none, even in highly worn teeth (41372-283). With extreme wear, a heavy facet appears on the lingual face of the hypocone, presumably the contact with the metaconid of M_3 (-306).

There is little or no hypocone on M^3 (fig. 3 J-K). The anterior half of the tooth is similar to that of the anterior molars, with a fairly large protostyle, normally as large as the hypocone, although the latter cusp is larger in 41372-288. The protoconule is clearly distinguishable. There is usually an elongate mesostyle, which is continued into a marginal crest that runs backward and lingually around the tooth. This crest is subdivided into a number of separate cuspules (fig. 3 J-L), the largest of which is the metacone. A metaconule usually extends from the metacone into the central basin, widely separated from both the protocone and the hypocone, but close to the posteroloph with which it would at least sometimes (fig. 3 J) unite after wear. One tooth is somewhat smaller than the other third molars, with a larger hypocone and no trace of a metaconule (fig. 3 L). It is possible that this

represents a different rodent, but it seems much more probable that it is merely an extreme variant of the *M. boskeyi* population. On at least some teeth, the antero-posterior diameter would decrease with wear, as the posteroloph overhangs the rear end of the tooth (fig. 3 J).

The trigonid of the lower cheek teeth is low crowned, in comparison with the talonid, for *Mysops*, but the difference between the two is much more striking than is the case in *Pareumys*, where the summits of all the crests reach essentially the same level, as in a dissected peneplain.

Only one specimen of P_4 is preserved. This, 41443-32, is the only specimen of *Mysops* from the basal conglomerate (fig. 4 A-B). This tooth is smaller than any of the molars, which may be because P_4 *is* smaller than any of the molars in *Mysops* (table 3), or may be because it came from a smaller animal, being from an earlier horizon, or both. The posterior arm of the protoconid runs into the middle of the posterolabial surface of the metaconid. The oval metaconid is high and far forward. The arm of the protoconid closes the trigonid basin, which drains anterad in typical *Mysops* fashion. The ectolophid is complete from the protoconid to the hypoconid. The hypolophid runs from the entoconid to the ectolophid, expanding at its middle into what may be termed an entoconulid. The hypoconid is large and hemispherical. The posterolophid reaches the base of the entoconid, but neither the posterior nor the central valley would be dammed until after very extensive wear.

The first molar is very typical of those of *Mysops*. The protoconid and metaconid are connected through an anterior cingulum that dams the anterior end of the trigonid basin (fig. 4 C-E). The posterior arm of the protoconid runs transversely from the protoconid, usually directly to the buccal side of the metaconid, but in some specimens (fig. 4 C) it curves forward to unite with the anterior cingulum buccal to the metaconid. Occasionally (fig. 4 D) there is essentially no posterior arm of the protoconid, so that the trigonid basin drains freely backward. The hypolophid may run directly across the tooth as is usual in *Mysops* (fig. 4 C; Wilson, 1938, figs. 8-9), or it may join the ectolophid in a smooth curve into the protoconid (fig. 4 D-E) as in *Pareumys* (Burke, 1935, fig. 4; Wilson, 1940a, pl. 1, figs. 6, 9; the continuity of the ectolophid into the protoconid of *Pareumys troxelli* is even more pronounced than Burke's figure would indicate). The middle of the hypolophid is sometimes enlarged into an entoconulid (fig. 4 C-D). There often is a suggestion of a mesoconid (fig. 4 C, E), but it seems merely to be the result of wear at the point where three crests meet rather than a distinct cusp, as it does not show up as an enlargement in unworn teeth (fig. 4 D). This is, very probably, the way in which mesoconids generally originated in rodents. The posterolophid expands into a hypoconulid, which may not be clearly visible until after wear. The hypoconid of the molars has developed considerable hypsodonty, not seen on the premolar, but much less than occurs in *Pareumys*, even *P. troxelli*. Even after very considerable wear, the lingual valleys are not fully dammed (41372-145); by the time that they do become closed, the buccal valley may also become a lake (fig. 4 E). With extreme wear, the buccal sides of the protoconid and hypoconid are worn well below the flat surface of the rest of the tooth (fig. 4 E).

The pattern of M_2 is very similar to that of M_1. The alignment of the posterior arm of the protoconid is more uniform than in M_1, running to the posterobuccal corner of the metaconid (fig. 4 F-I). There is the same variability as in M_1 in the mesoconid, entoconulid, hypoconulid and alignment of the hypolophid. The hypo-

conid hypsodonty is pronounced (fig. 4 G). With wear, the trigonid basin becomes merely a dimple on the surface that slopes from the metaconid to the protoconid (fig. 4 I). As in M_1, there seem always to have been three roots, two anterior and one posterior, in contrast to the situation in *M. parvus*, where there is very great individual variation as to whether there are one or two anterior roots.

There is much more variability in the trigonid area of M_3 than in the other molars. The trigonid is high, with the metaconid its highest point (fig. 4 L). Usually the trigonid basin is closed anteriorly and open posteriorly (fig. 4 J-L), but sometimes the reverse is true (fig. 4 M-N and 41372-277). If the basin is closed, the posterior arm of the protoconid runs to the rear of the metaconid; if it is not, this arm is short (fig. 4 K) or perhaps even nonexistent (fig. 4 J). The course that would be taken by the posterior arm of the protoconid is marked, in some of these last specimens, by a backwardly directed ridge from the metaconid (fig. 4K). The posterior arm of the metaconid, along the lingual margin of the tooth, often enlarges into a metastylid (fig. 4 M-N).[5] There is no mesoconid, although in one unworn specimen the crest of the ectolophid is elevated at this position (fig. 4 L). There may or may not be an entoconulid, and the hypolophid varies, as in M_{1-2}, from being transverse to being a curved continuation of the anterior part of the ectolophid (fig. 4 J-N). The hypoconulid does not appear until after wear, when it forms a backwardly developing enlargement of the posterolophid (fig. 4 J-N). It may or may not be separated from the hypoconid by a valley down the posterior slope of the tooth. In several specimens (fig. 4 J-M) the lingual marginal crest is continuous from the metaconid to the entoconid, closing off the central valley. In others (fig. 4 N), the valley is open. The posterior valley is never as fully dammed. There are three roots, arranged as in M_{1-2}. The posterior root may be anteroposteriorly elongate in cross section.

The wear of one specimen of M_3 is unusual (fig. 4 J). The protoconid is highly worn, with several irregularities in its outline. The posterior arm of the metaconid and the entoconid are united, and there is a broad, continuous wear surface, sloping lingually, from the front of the metaconid to the rear of the entoconid. Most of the top of the entoconid has been incorporated into this wear surface, leaving only a V-shaped portion of the usual flat wear surface. The oblique wear surface is nearly continuous with another sloping surface worn onto the rear of the posterolophid.

A number of isolated incisors are referred to this species by elimination. The lower incisors of *Prolapsus* can be identified because one is present in the holotype jaw. Of the remaining lower incisors in the collection, only one is of the correct size to belong to *M. boskeyi*, and it agrees with the lower incisors of *Mysops* (Wilson, 1938, p. 208) and of *Pareumys troxelli* in being generally flattened on the anterior face (fig. 3 Q). The upper incisors that are included here are similar to the lower in size and enamel thickness, have considerably thinner enamel than do those referred to *Prolapsus*, are of the correct size to belong with the upper teeth of

[5]Dawson (1966, p. 101, footnote) points out the difficulty of distinguishing between what have been called metastylid and mesostylid (Wood and Wilson, 1936), especially when only one is present. I have tried to distinguish between them on the same basis that she suggested, namely that the metastylid is an enlargement of the posterior arm of the metaconid along the lingual margin of the tooth, usually in front of the opening of the central valley, whereas the mesostylid is independent of the posterior arm of the metaconid and tends to block the opening of the central valley.

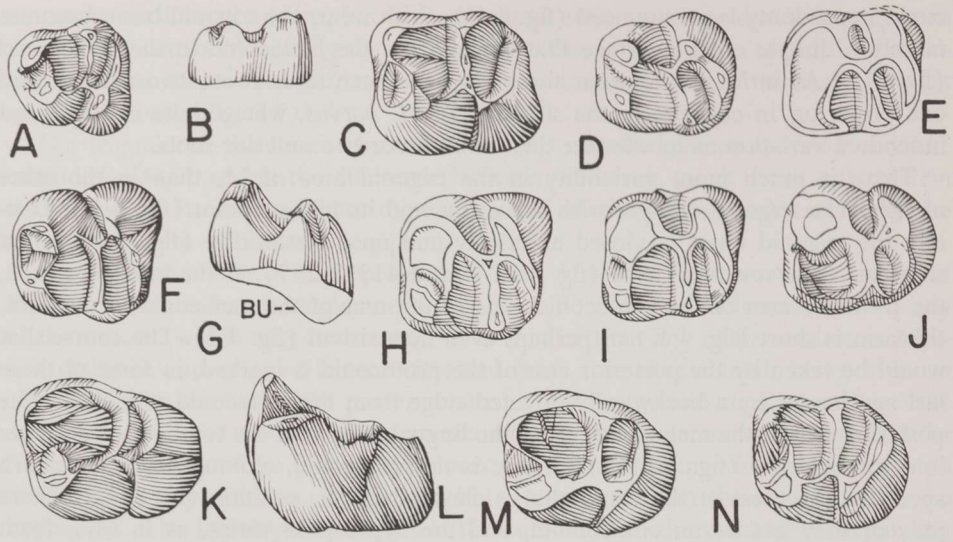

Fig. 4. Lower cheeck teeth of *Mysops boskeyi*, new species, X 10.

A. LP_4, 41443-32. B. LP_4, -32, lingual view. C. LM_1, 41372-257. D. RM_1, -293. E. RM_1, -275. F. RM_2, -272. G. RM_2 -272. Lingual view. BU = lower limit of enamel on buccal side, seen from inside. H. RM_2, -251. I. RM_2, -268. J. RM_3, -258. K. LM_3, -273. L. LM_3, -273. Buccal view. Bottom of drawing is base of enamel. M. LM_3, -253. N. LM_3, -250.

Mysops boskeyi, and are sufficiently abundant so that they must have belonged either to *Mysops* or to *Prolapsus*. These upper incisors have a rounded anterior face, which sometimes is nearly flat (fig. 3 M, O, P). The enamel extends well onto the lateral surface, and the pulp cavity is comma-shaped. The enlargement of this tooth in juveniles was very rapid, one specimen (41372-241) increasing its diameters about 20% in a distance of 5.1 mm along the outer curve of the tooth, and an even younger incisor (-241D, fig. 3 O) increasing about 15% in a distance of 2.2 mm (table 4). The lingual enamel is more limited in the juveniles than in adults. With increasing age, the enamel thickens slightly (fig. 3 P).

Two upper incisors show faint markings along the lingual surface of the dentine (fig. 3 N), of the type previously interpreted as diurnal growth lines (Wood, 1970, fig. 6 C and p. 248-249). There are twelve of these lines in a distance of 4.3 mm on 41372-243C, and 20 in 6.2 mm on -241B (fig. 3 N). If these are diurnal growth lines, it would indicate a growth rate of 2.2—2.5 mm per week, reasonable rates for the upper incisors of a small rodent. However, these values are low enough to imply, by contrast with the rates in *Geomys* (Manaro, 1959), that *Mysops* had not developed significant burrowing tendencies, in contrast to what has generally been assumed for the Oligocene cylindrodonts.

DISCUSSION

This species is clearly related both to *Mysops* and to *Pareumys*, especially to *P. troxelli*. It agrees with both in the incomplete metaloph, the weak protoconule, the poorly developed hypocones, the distinct lingual hypsodonty of the upper teeth, the course of the posterior arm of the protoconid, and the flattening of the anterior face of the lower incisor.

It is most like *Mysops* in the overall low crowns, in the considerable excess of trigonid height over talonid height, in the frequent closing of the posterior valleys in the lower teeth, and in the frequent absence of posterior closure of the trigonid basin. On the other hand, it agrees with *Pareumys troxelli* in the advanced stage of connection of the metaloph to the posteroloph (even though it sometimes would unite, at a late stage of wear, with the protocone), the better developed hypocones and the frequent presence of entoconulids. On the whole, it is closest, among hitherto described rodents, to *Mysops parvus* (Wilson, 1938, p. 207-217), and there does not seem to be any valid basis, at present, for separating it from *Mysops*. *Mysops boskeyi* does, however, show many features suggestive of *Pareumys troxelli*, and it was probably close to the ancestry of that species. Burke stated (1935, p. 10) that *P. troxelli* was sufficiently different from the other (later) species of the genus so that he was hesitant about including it in *Pareumys*. He compared it with *Tillomys* rather than with *Mysops*, as the then latest work on small Bridgeran rodents (Troxell, 1923) included in *Tillomys* much of what Wilson (1938, p. 207-217) later placed in *Mysops*. The markedly lower crowns in *M. boskeyi* than in any species of *Pareumys*, together with the noticeable excess of trigonid height over talonid height, indicate that this species fits better in *Mysops* than in *Pareumys*. *Tillomys*, as distinguised by Wilson (1938, p. 217-222) is clearly a very distinct type of rodent.

If the Texas species is correctly referred to *Mysops*, it is much more advanced in its cheek tooth characteristics toward *Pareumys* than any of the previously described species. It is also considerably larger than *M. parvus* (tables 3-5) in its cheek tooth measurements. Calculations of s and V for *M. boskeyi* are not given because of the unreliability of s based on such a small sample. They were calculated, however, and t-tests run on the results indicate that, in general, the probability that *M. parvus* and *M. boskeyi* are part of the same population is less than .001, although for P_4 (represented by one tooth) the probability is higher, but less than .02 for all three measurements. A more reliable comparison showed that the 12 sample means for the lower cheek teeth of *M. boskeyi* exceed the corresponding ones of *M. parvus* by amounts equal to 2.1-4.6 of the s for *M. parvus*, with an average of about 3.2 s. The individual measurements of *M. boskeyi* exceed the $\overline{X}$ of *M. parvus* by amounts equal to 1.2-8.0 s. The only measurements that do not show a considerable excess in size of *M. boskeyi* are those of the lower incisors, where the anteroposterior diameter of the Texan specimen is 1.4 s larger, the transverse diameter is the same, and the ratio is 1.8 s smaller. That is, *M. boskeyi* was larger than *M. parvus*, but seems to have had much more slender lower incisors. Wilson (1938, p. 210, 212-213) indicated that *Mysops minimus* and *M. fraternus* could not be separated from *M. parvus* on the basis of size. The material from Texas does not differ greatly in size from the holotype of *Pareumys troxelli* (cf. tables 4-5 and Burke, 1935, p. 12) from the early Uintan, although it is clearly more primitive in tooth pattern.

The sequence *Mysops-Pareumys-Jaywilsonomys* seems to be a true phyletic sequence. The Texan *Mysops boskeyi* could readily have been ancestral, perhaps through unknown late Eocene Texan or Mexican species of *Pareumys*, to the early Oligocene Chihuahuan *Jaywilsonomys* (Ferrusquia and Wood, 1969, p. 6). The closest described species of *Pareumys* to this phyletic line would seem to be *P. troxelli* from Utah.

FAMILY INDET.

Prolapsus,[6] new genus

Genotype.—*Prolapsus sibilatoris,* new species.

Referred species.—Genotype and *P. junctionis*, new species.

Diagnosis.—Fully hystricognathous, with angle arising entirely laterad of incisive alveolus; lower premolar smaller than molars; lower cheek teeth with transversely elongate and progressively subdivided mesoconid; molar metalophid extending from protoconid to rear surface of metaconid, closing rear of trigonid basin; anterior cingulum bearing an anteroconid; usually a forward opening of trigonid basin at one or both ends of anterior cingulum; lower teeth with partial or complete crests from entoconid toward hypoconid, often with a cusp-like enlargement in the center of the crest; posterolophid reaching to or nearly to entoconid and usually with one or more prominent hypoconulids; only incipient lingual hypsodonty in upper cheek teeth; quadrate upper molars with large and distinct hypocone; protoloph usually complete after moderate wear; anterior cingulum large with strong lingual protostyle; anterior arm of hypocone widely separate from protocone and protoloph, and continuous into central basin, almost to paracone, forming a pseudomesoloph; single or multiple metaconules connecting with hypocone in varying manners; strong posterior cingulum; prominent mesostyles; protocone and hypocone of P^4 not separated and tooth subtriangular; lower cheek teeth with two roots, one anterior and one posterior; upper cheek teeth with two buccal and one lingual roots; lower incisor with flat anterior face, enamel extending well onto lateral side, but widest point just behind the enamel cap; incisor enamel pauciserial as in paramyids, sciuravids, and Eocene cylindrodonts; tooth measurements as given in tables 6-7.

Distribution.—Basal part of Pruett Formation, Middle Eocene, Big Bend region of Texas.

DESCRIPTION

The most striking feature of *Prolapsus* is the fully hystricognathous character of the lower jaw, as described previously (Wood, 1972, p. 1250-1251). The masseteric fossa of the mandible is deep (fig. 5 A), and, at its ventral side, lies well lateral to the cheek teeth and to the lower incisor (fig. 6 A). In the ventral view, this extension is seen to arise from the side of the incisive alveolus (fig. 6 B, I-I), in the manner that is termed hystricognathous. The dorsal border of the masseteric fossa, marking the insertion of the *masseter medialis*, is low on the jaw, well below the alveolus of M_3, and curves upward, behind that tooth, into the ascending ramus and the front of the coronoid process, which rises steeply, reaching a level well above that of the occlusal surface. The area behind the anterior margin of the coronoid process is badly broken and crushed, and its details are uncertain. There is a single mental foramen just in front of P_4 (fig. 5 A). The chin process is rather prominent. On the medial surface, the genioglossal pit is large (fig. 5 B). Breakage in the posterior region prevents any inferences about the insertions of the muscles in this area.

The three lower molars are preserved in the holotype of *P. sibilatoris* (fig. 6 G).

[6]From Latin, "*In genua prolapsus*," a squat, in reference to Whistler Squat, the main locality whence the specimens came.

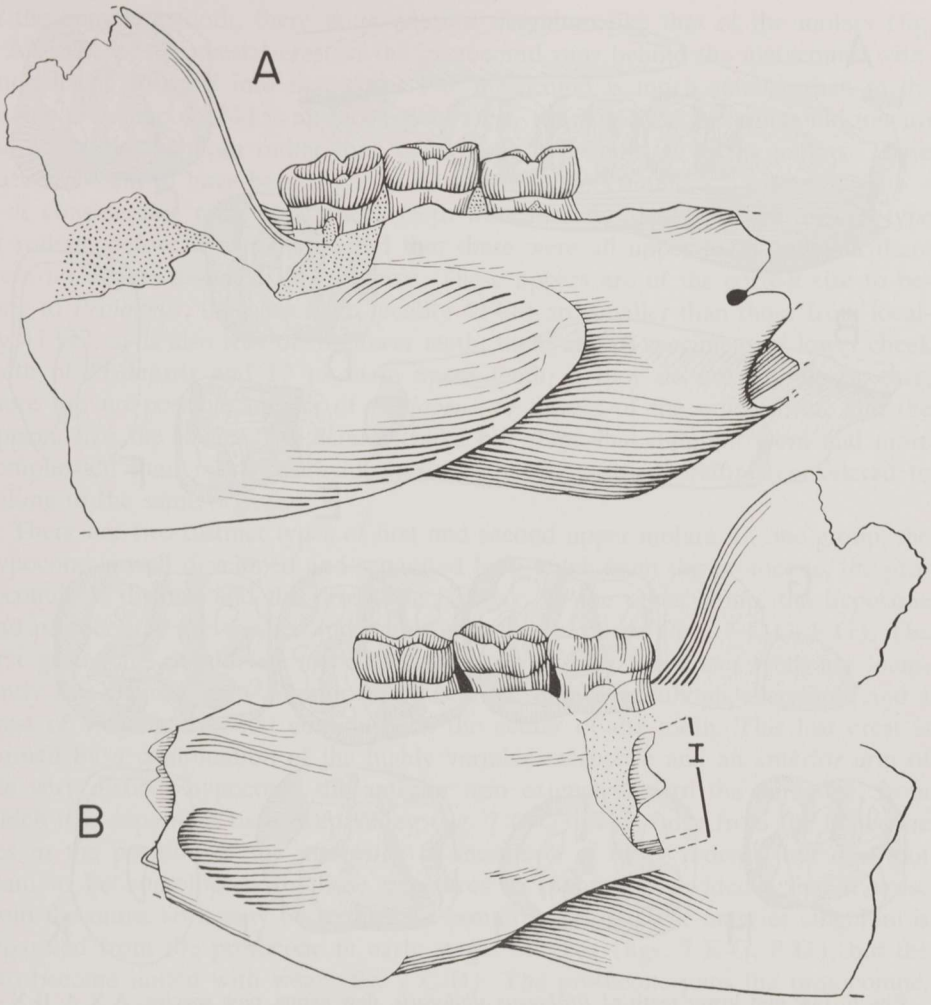

Fig. 5. Jaw of *Prolapsus sibilatoris*, new genus, new species. Holotype, 41372-179, ca. X 5. Posterior parts of jaw badly broken.

A. Lateral view of lower jaw. B. Medial view of lower jaw. I = posterior end of lower incisor.

Each has a prominent metaconid, extending backward as a lingual crest. The much lower protoconid connects with the posterior or lateral side of the metaconid, closing off the trigonid basin. An anterior cingulum, often enlarging into an anteroconid, runs across the anterior end of the tooth, but the trigonid basin normally drains freely around one or both ends of the cingulum. The mesoconid is large, and is usually double. The buccal part is larger, the anterior cingulum nearly closes the trigonid basin, the hypolophid connects with the hypoconid after little or no wear, and the posterior cingulum is weakly connected with the entoconid, on M_1 of 41372-179. The buccal mesoconid is smaller, the trigonid basin opens freely anteriorly, the hypolophid is not complete before wear, and there is a strong connection of the entoconid and posterior cingulum of M_2. These differences have been used to identify isolated teeth as M_1 and M_2, respectively.

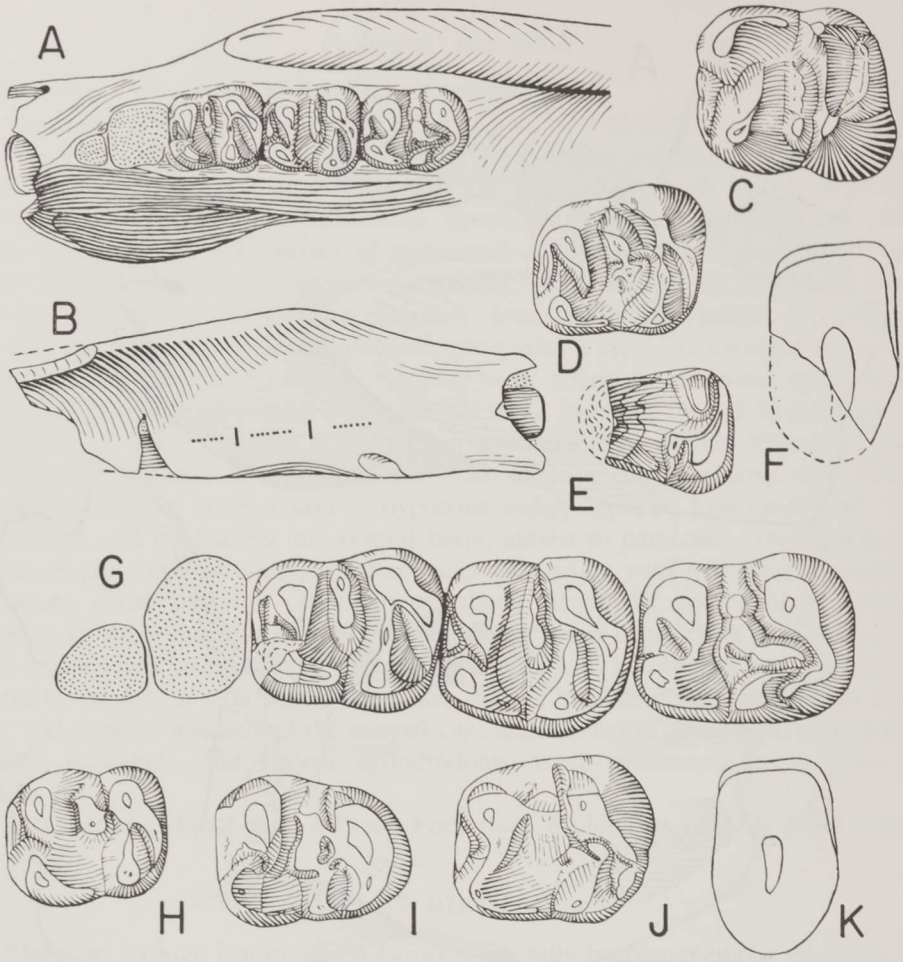

Fig. 6. Jaw and lower teeth of *Prolapsus sibilatoris*, new genus, new species. A X 5; B X 4; others X 10.

A. Dorsal view of lower jaw, holotype, 41372-179. Broken rear portions omitted. B. Ventral view of lower jaw, holotype, -179. I-I = incisive alveolus. C. LM_1, -284. D. RM_1, -291. E. LP_4, -299, anterior tip restored from 41444-1. F. Cross section of RI_1 seen from the front, holotype, 41372-179. Outline of tooth restored from the shape of the alveolus. G. RM_{1-3} and alveolus of P_4, holotype, -179. H. RM_2, -266. I. RM_3, -265. J. RM_3, -269. K. Cross section of RI_1, -241C, from the front.

The third lower molar differs from the two anterior ones in the arrangement of the crests of the talonid basin. The hypolophid is incomplete in most specimens (figs. 6 G, J; 8 D, J), only one (fig. 6 I) showing a continuous connection from the entoconid to the hypoconid. The large mesoconid has varying connections with the central part of the hypolophid (figs. 6 G, I, J; 8 D, J), and this last may be directed toward one of the hypoconulids rather than toward the entoconid (figs. 6 G; 8 D).

Two isolated teeth, one broken, have been identified as P_4 of this genus, a tooth considerably smaller than the molars. The metaconid is very high (fig. 6 E) and,

in the complete tooth, there is an anterior cingulum like that of the molars (fig. 8 A). The posteromesial crest of the protoconid runs behind the metaconid, without curving forward into that cusp. The mesoconid is much smaller than in the molars. The hypolophid is an incomplete crest, running from the entoconid toward the posterior cingulum rather than toward the hypoconid as in the molars. There does not seem to have been a particularly strong hypoconulid.

A considerable number of cheek teeth were initially identified as a distinct type of rodent, before it was discovered that these were all upper teeth and that there were no uppers assigned to *Prolapsus*. These uppers are of the correct size to belong to *Prolapsus*; the ones from locality 41444 are smaller than those from locality 41372, as is also true of the lower teeth; there are 14 specimens of lower cheek teeth of *Prolapsus* and 17 of these upper teeth; if they do not belong together, there are no possible uppers of *Prolapsus* or lowers of the other form; and the uppers, like the lowers, are sciuravid-like but somewhat different from and more complicated than most sciuravid cheek teeth. They are, therefore, considered to belong to the same organism.

There are two distinct types of first and second upper molars. In one group, the hypocone is well developed and separated by a notch from the protocone, the protoconule is distinct and the protostyle is weak. In the other group, the hypocone and protoconule are weaker and the protostyle is stronger (figs. 7 C-G, 8 G). The first group are considered to be M^1; the second, M^2. The upper teeth are incipiently five crested, with anterior and posterior cingula, protoloph, metaloph, and a crest of varying size and continuity in the center of the tooth. This last crest is formed by a combination of the highly variable mesostyle and an anterior arm of the very distinct hypocone; the anterior arm extends toward the paracone, from which it is separated by a deep valley (fig. 7 C-G). This ridge from the hypocone lies in the position of the mesocone or mesoloph of other rodents, but does not seem to be homologous to those structures as there is no evidence that it arose from the mure, so it may be termed the pseudomesoloph. The anterior cingulum is separated from the protocone in early stages of wear (figs. 7 E-G, 8 G), but the two become united with wear (fig. 7 C-D). The protocone joins the protoconule, which may unite directly with the paracone (fig. 7 C), may run independently along the front of the paracone (figs. 7 D, 8 G), may do both (fig. 7 E), or may do neither (fig. 7 F). The unworn protoconule usually consists of two separate cuspules (figs. 7 E, 8 G). The pseudomesoloph, of varying complexity, is always isolated from the metaconule by a deep valley, whereas the separation of the metacone and metaconule may be either deep (fig. 7 E, G) or shallow (figs. 7 F, 8 G). With wear, the metaconule may connect directly with the hypocone, but it usually unites first with the pseudomesoloph (figs. 7 C, D, F; 8 G).

Only one tooth considered to be M^3 of this genus was found (fig. 8 H). The anteroloph and protoloph are essentially similar to those of M^{1-2}. A continuous crest bounds the posterior part of the tooth, with several cusp-like enlargements visible on it. The buccal margin is formed by two mesostyles; there is a large metacone at the rear of the tooth. Linguad of the metacone are two elongate expanded areas, one adjacent to the metacone and presumably homologous to the posteroloph of the anterior molars, and the other, presumably the hypocone, just behind the protocone. Ridges extend from each of these elements into the central basin, including a complex area related to the mesostyles, an anteriorly directed crest from

TABLE 6
Measurements (in mm) of lower teeth of *Prolapsus*

	P. sibilatoris													*P. junctionis*							*Prolapsus* sp. indet.
	41372													41443	41444						41444
	Holotype -179 R	-143 L	-241C R	-265 R	-266 R	-269 R	-284 L	-291 R	-299 L	N	$\bar{X}'$	s'	$\bar{X}'-3s'$	-33 L	-1 R	-59 L	-61 L	Holotype -62 R	-65 L		-60 R
P_4-M_3 anteroposterior	alv. 10.35																				
P_4 anteroposterior	alv. 2.5								±2						1.56						
width, metalophid									1.26	1	1.26				1.26						
width, hypolophid									1.62	1	1.62				1.57						
M_1 anteroposterior	2.52						2.66	2.23		3	2.47±.13		2.08	1.91				1.91			
width, metalophid	1.92						2.18	1.74		3	1.95±.10		1.65	1.51				1.68			
width, hypolophid	2.15						2.26	1.94		3	2.12±.11		1.79	1.63				1.83			
M_2 anteroposterior	2.52				2.10					2	2.31±.12		1.95			2.08					
width, metalophid	2.12				1.80					2	1.96±.10		1.66			1.75					
width, hypolophid	2.36				1.74					2	2.05±.10		1.75			1.90					
M_3 anteroposterior	2.85	2.69		2.63		2.61				4	2.70±.14		2.28				2.27		2.20		1.30
width, metalophid	2.08	1.92		2.00		2.07				4	2.02±.10		1.72				1.85		1.73		1.21
width, hypolophid	2.20	1.71		1.78		2.20				4	1.97±.10		1.67				1.81		1.60		1.18
I_1 anteroposterior	±2.9		2.60							2	2.75										
transverse	1.72		1.66							2	1.69										
ratio			.64							1	.64										

$\bar{X}'$ = assumed mean of the population of *P. sibilatoris*, is the actual mean of the available specimens.

s' was calculated, assuming V to have been 5.00 (a high value for cheek teeth of Eocene rodents) from the formula $V = \frac{100s'}{\bar{X}'}$

the metacone that enlarges into a metaconule, a crest at right angles to the posteroloph, and several irregularities arising from the hypocone and protocone.

Three teeth are considered to be P^4 of *Prolapsus* (figs. 7 A-B, 8 F). In these, the protoloph is essentially like that of the molars. There is a variable amount of separation of the protocone and hypocone, but they are never as distinct as in M^{1-2}. The mesostyle is large, elongate in two specimens (fig. 7 A-B), and runs toward a crest that may unite with the hypocone, the protocone, or the metaconule. The metacone is little if any larger than the mesostyle and the metaloph is interrupted at early stages of wear. The posteroloph is more prominent than the metaloph.

Two lower incisors, one in the jaw of the holotype of *P. sibilatoris*, are referred to this genus. The anterior face is flat (fig. 6 F, K), and the enamel extends well around onto the lateral face. The widest part of the tooth is just behind the enamel cap, which curves outward to reach this area. The pulp cavity is comma-shaped in cross section. Two isolated upper incisors, similar to the lowers in their flat anterior faces, enamel thickness and enamel distribution (figs. 7 H, 8 E), are tentatively referred to this genus. The incisor enamel, of both upper and lower incisors, is of the pauciserial type (Wahlert, 1968, p. 4, and fig. 1 C). In this respect, *Prolapsus* resembles paramyids and sciuravids and the Bridgeran *Mysops* (Wahlert, 1968, pp. 14-15), and is very different from all known caviomorphs. It differs from the usual pauciserial condition (Wahlert, 1968, p. 4) in that the enamel bands of the lower incisors are inclined toward the tip of the incisor at an angle of 19° and those of the uppers at an angle of 15°.

DISCUSSION

The importance of the discovery of a hystricognathous rodent jaw from the Eocene of Texas has previously been pointed out (Wood, 1972). The determination of its possible relationships is equally important.

As indicated above, the lower jaw of the *Prolapsus* is completely hystricognathous, with the angle arising well laterad of the incisive alveolus. The hystricognathy is as fully developed in this specimen as in any of the South American or Old World hystricognath rodents, and is much more advanced than in its contemporary, *Reithroparamys* (cf. figs. 5-6 and Wood, 1962, figs. 41 E, 46 B). *Prolapsus* is the only fully hystricognathous rodent hitherto recognized from the Eocene of any part of the world. As far as this single character is concerned, *Prolapsus* could easily have been ancestral to all the later hystricognathous rodents of the entire world, including the South American Caviomorpha, the African Phiomorpha and the Old World Hystricidae.

Elsewhere in the Rodentia, complete hystricognathy is always[7] accompanied by an enlarged infraorbital foramen, through which (except in *Platypittamys*—Wood, 1949, fig. 2 A) the origin of the *masseter medialis* migrates forward onto the side of the snout. Hystricognathy is also accompanied (Woods, 1972, fig. 2 A) by a backward growth of the *masseter lateralis profundus, pars posterior*, deep division, which inserts, on the posterior margin of the ascending ramus just below the condyle, on a pronounced postcondylar process.

[7]Except in the Bathyergidae, where unpublished work by Lavocat suggests that there has been secondary reduction in the size of the infraorbital foramen and of its associated portion of the *masseter medialis*.

TABLE 7

Measurements (in mm) of upper teeth of *Prolapsus*

	Prolapsus sibilatoris, n.g., n.sp., 41372															*P. junctionis*, n. sp. 41443		41444	*Prolapsus*, sp. indet. 41372-279	
	-241G R	-252 R	-256 L	-262 R	-263 L	-278 L	-285 R	-295 R	-297 R	-300 L	-304 L	N	$\bar{X}'$	s'	$\bar{X}'$ -3s'	-30 R	-25 R	-26 L	-56B L	R
P^4 anteroposterior						2.28			2.22			2	2.25±.11	1.92				1.40		1.33
width, protoloph						2.52			2.63			2	2.58±.13	2.19				1.83		1.42
width, metaloph						2.47			2.60			2	2.54±.13	2.15				1.70		1.38
M^1 anteroposterior			2.20	2.25			2.32			2.27		4	2.26							
width, protoloph			2.53	2.4			2.51			2.57		3	2.54							
width, metaloph			2.42	2.3			2.45			2.43		3	2.43							
M^2 anteroposterior		1.6+			2.21			2.09			2.28	3	2.19±.11	1.86			1.78			
width, protoloph		1.75+			2.43			2.34			-------	2	2.39±.12	2.03			1.95			
width, metaloph		1.6+			2.21			2.13			-------	2	2.17±.11	1.84			1.88			
M^3 anteroposterior																2.19				
width, protoloph																2.13				
width, metaloph																2.00				
I^1 anteroposterior	2.30																		1.89	
transverse	1.50																		0.99	
ratio	.65																		.53	

$\bar{X}'$ = assumed mean of the population of *P. sibilatoris*. is the actual mean of the available specimens.

s' was calculated, assuming V to have been 5.00 (a high value for cheek teeth of Eocene rodents) from the formula $V = \frac{100s'}{\bar{X}'}$.

In view of the fragmentary nature of the specimen of *Prolapsus*, nothing can be told of the condition of the infraorbital foramen (= origin of *masseter medialis*) or of the postcondylar process (= insertion of *masseter lateralis profundus, pars posterior*, deep portion). One might be tempted to try to draw inferences, were it not for the number of exceptional rodents that are already known—the hystricomorphous but thoroughly sciurognathous theridomyoids, anomalurids, ctenodactylids and pedetids; the subhystricognathous but protrogomorphous *Reithroparamys;* the hystricomorphous but apparently sciurognathous *Protoptychus*; and the hystricognathous *Platypittamys* in which the masseter had not yet invaded the moderately enlarged infraorbital foramen. We must, therefore, restrict all interpretations of the relationships of *Prolapsus* to the available material, even though it might be tempting to do otherwise.

The mandibles of the holotypes of *Pauromys perditus* and *P. schaubi* are unfortunately broken so that it is impossible to determine whether or not they were hystricognathous, but no evidence of hystricognathy has been reported in any sciuravid. Dr. Mary Dawson informed me (*in lit.*, 10 May 1972) that the mandibles of *Pauromys* sp. (in particular, that of Carnegie Mus. 19568) show no indications of hystricognathy, incipient or otherwise.

The strength and angulation of the crest for the insertion of the *masseter medialis* are very similar to those in the contemporaneous *Pauromys schaubi* (Wood, 1959, fig. 1 C) and possibly to those in *Tillomys senex* (Wilson, 1938, fig. 11), but are quite different from those in most sciuravids (*Sciuravus nitidus*, Dawson, 1961, pl. V; *Sciuravus powayensis*, Wilson, 1940b, pl. 1, fig. 3; *Pauromys perditus*, Dawson, 1968, fig. 40). This part of the mandible is very reminiscent of such caviomorphs as *Platypittamys* (Wood, 1949, fig. 2 B) or *Deseadomys* (Wood and Patterson, 1959, fig. 6). *Prolapsus* differs, in the relative weakness of this ridge, from the jaws of *Cephalomys* (Wood and Patterson, 1959, fig. 22 C) and *Sallamys* (Patterson and Wood, in preparation).

The single mental foramen is a distinction from *Sciuravus* and *Deseadomys*, where there are small accessory foramina, but agrees with *Tillomys* (Wilson, 1938, fig. 11), *Pauromys* (Dawson, 1968, p. 358) and *Platypittamys* (Wood, 1949, fig. 2 B). The prominent chin (fig. 5 A, B) is as in *Pauromys*, *Tillomys*, *Platypittamys*, *Deseadomys* and *Scotamys*.

The fragments of the badly broken ascending ramus suggest that *Prolapsus* did not have the long, slender coronoid process seen in many caviomorphs, this region probably having been much like that of *Platypittamys* (Wood, 1949, fig. 2 B).

The cheek teeth of *Prolapsus* seem clearly to be of sciuravid derivation. The lower teeth are particularly reminiscent of those of *Pauromys* (Wood, 1937, fig. 65; 1959, fig. 1 A; Dawson, 1968, figs. 39, 48–54) in the large anterolophid and the transversely elongate mesoconids. However, P_4 of *Prolapsus*, although small, is proportionately much larger than in *Pauromys,* and the hypoconid and entoconid of the lower molars of *Pauromys* unite through the posterior cingulum rather than directly as is usual in *Prolapsus*. In no sciuravids other than *Pauromys*, so far as I am aware, are there such elongate anterior cingula and mesoconids. Similar cingula are present in *Microparamys*, but the remainder of the tooth pattern is not especially like that of *Prolapsus*.

The upper cheek teeth are rather different from those referred by Dawson (1968, p. 355-358, figs. 41-47) to *Pauromys* sp., the only upper teeth known from that

genus. The anterior cingula are more distinct in *Pauromys*, the paracone and protocone are directly connected with at most a faint protoconule, and there does not appear to have been a pseudomesoloph in *Pauromys*, the anterior arm of the hypocone curving into the metacone to form the metaloph (Dawson, 1968, figs. 41, 43-44). There is more connection of the protocone and hypocone in *Pauromys* than in *Prolapsus*. The hypocone of P^4 of *Pauromys* is much better developed than is that of *Prolapsus* (cf. Dawson, 1968, p. 355), but the tooth in general is distinctly more molariform in *Prolapsus*. It is difficult to be certain, but the third molars of the two do not seem to show much similarity except that both have rather complicated patterns. The upper teeth of *Prolapsus* differ from those of *Sciuravus* and *Tillomys* (Dawson, 1968, figs. 21-38; Wilson, 1938, figs. 1-3, 11; Wood, 1937, figs. 13-16) in the development of incipient fifth crests and the weak protocone-hypocone connection.

The lower teeth of the Uintan *Protoptychus* have never been described. The upper teeth, however, clearly are four-crested, with no trace of either a mesoloph or a pseudomesoloph (Wilson, 1937, fig. 1), and it seems probable that the same basic pattern was present in the lowers.

The presence of at least incipient mesolophids and pseudomesolophs in *Prolapsus* is a clear distinction from the incipiently four-crested late Eocene *Rapamys* and *Tapomys* (Wood, 1962, figs. 52-53) as well as from the four-crested South American *Platypittamys* (Wood, 1949, fig. 3), *Deseadomys* (Wood and Patterson, 1959, fig. 4) and *Xylechimys* (Patterson and Pascual, 1968). If, as seems probable, Wood and Patterson (1959, p. 389 *et seq.*) were correct that *Platypittamys* and *Deseadomys* possessed the most primitive known caviomorph dentitions, these genera were clearly more primitive in their tooth pattern than was *Prolapsus*.

There are no similarities in the teeth (except that both show five crests, but of very different types) between *Prolapsus* and the phiomyids from the early Oligocene of Egypt (Wood, 1968, figs. 1 A; 2 C, G; 4 B; 7; 14 C; 16).

The cross section of the lower incisor is quite different from that of *Pauromys schaubi* (Wood, 1959, fig. 1 B), and apparently also from that of *Pauromys* sp. (Dawson, 1968, p. 359). Likewise, it is quite unlike those of any known caviomorphs (Wood and Patterson, 1959, figs. 5 B, 7 B, 10 A-B, 20 C, 23 B). It is, however, rather similar to that of *Sciuravus eucristadens* (Dawson, 1968, fig. 20). In enamel histology, the pauciserial teeth are like those of paramyids, sciuravids and the Bridgeran *Mysops* (Wahlert, 1968, pp. 14-15), thus falling into the group that have the primitive pattern for the rodents. Unfortunately, the enamel histology has not been reported for any member of the Reithroparamyinae. Although they are pauciserial, the incisors show an advance from the typical condition, toward either the uniserial or the multiserial pattern, in the marked inclination of the enamel bands.

These comparisons lead to the question of the phyletic relationships of *Prolapsus*. Obviously, there are a number of groups that must be considered as possible relatives. These include the North American Reithroparamyinae, Sciuravidae (especially *Pauromys*) and Protoptychidae; *Floresomys* and *Guanajuatomys* from Mexico; the Eocene to Oligocene Theridomorpha of Europe; and the early Oligocene Caviomorpha of South America and Phiomyidae of Egypt.

The first evidence discovered of hystricognathy in Eocene rodents is the very incipient condition (the angular process just lateral to the plane of the incisor, but

only just lateral to it) in *Reithroparamys* (Landry, 1957, p. 82; Wood, 1962, p. 122). This condition occurs in several other paramyids (*Franimys*, *Rapamys* and *Tapomys*), and was used by Wood (1962, p. 117) as a diagnostic feature of the Subfamily Reithroparamyinae. The members of this subfamily also show well developed (but not complete) hypolophids, but differ markedly from *Prolapsus* in a number of respects:—the trigonid basins open posteriorly; the ectolophids are complete anteroposteriorly; the mesoconid is at most a slight swelling of the ectolophid and is never transversely elongate; hypoconulids are poorly developed on M_{1-2}; the hypocone is never fully separated from the protocone; the anteroloph joins the protocone; there is never any indication of a pseudomesoloph arising from the hypocone; and the mesostyles are not transversely elongate. The entire cheek tooth structure of *Prolapsus* is much more sciuravid than paramyid, and *Prolapsus* could not be placed in the Paramyidae without a complete redefinition of that family, probably involving the union of the Paramyidae and Sciuravidae.

The dental similarities between *Prolapsus* and the Sciuravidae (especially *Pauromys*) have been discussed above. Were only the teeth of *Prolapsus* known, there would be no problem in placing it in the Sciuravidae, but the complete hystricognathy of *Prolapsus*, a feature not even hinted at in any known sciuravid, makes its allocation to the Sciuravidae impossible. There does not, however, seem to be any reason for not considering that the ancestors of *Prolapsus* were early Eocene sciuravids.

There is no resemblance of *Prolapsus*, either in the teeth or the jaw, to the peculiar *Floresomys* from the Eocene of Guanajuato, as described by Fries, Hibbard and Dunkle (1955, p. 16-23 and fig. 6), or to the hystricognathous *Guanajuatomys* from the same deposits (Black and Stephens, 1973).

If the skull of *Prolapsus* should prove to have been hystricomorphous, it might be possible to refer it to the Protoptychidae, where Wahlert (*in lit.*, Aug. 11, 1972) reports that there has been invasion of the infraorbital foramen by the *masseter medialis*, but that the mandible is apparently not hystricognathous. The cheek teeth of *Prolapsus*, however, seem much more like those of sciuravids than like the few that have been described for *Protoptychus*, especially in view of the general simplicity of the cheek teeth of *Protoptychus* and the absence of any suggestion of a fifth crest in that genus (Wilson, 1937, fig. 1). Furthermore, since we have no knowledge of whether or not *Prolapsus* was hystricomorphous, and since *Protoptychus* probably was not hystricognathous, placing the former in the Protoptychidae would not be advisable at the present time.

The European Theridomorpha (Pseudosciuridae and Theridomyidae) are hystricomorphous but show no suggestion of hystricognathy, and there seems no basis for considering them related to *Prolapsus*. The same is true for the Old World Anomaluridae, Ctenodactylidae and Pedetidae.

There is no conceivable possibility of placing *Prolapsus* in any of the numerous families of Caviomorpha represented in the Deseadan of South America (Wood and Patterson, 1959; Patterson and Wood, in preparation); in any family of the African Phiomorpha (including the Bathyergidae); or in the Hystricidae. No other families of hystricognathous rodents are known.

Although an author should do his best to assign a new genus to a family, I have left *Prolapsus incertae sedis* as to familial and superfamilial allocation, pending the discovery of more complete materials, including, specifically, the posterior part of

the mandible and the snout, including the infraorbital foramen. The present evidence does not warrant the assignment of *Prolapsus* to any known family, and a new family erected to receive it could not be adequately defined on the basis of the known material.

With the description of *Prolapsus*, there are not only incipiently hystricognathous (Reithroparamyinae) but also fully hystricognathous Eocene rodents known from North America, the only place in the world where such have been reported.[8] The middle Eocene Reithroparamyinae were not hystricomorphous; the status of the infraorbital foramen in late Eocene members of the subfamily is not certainly known, although the very fragmentary specimen of *Rapamys* (Wood, 1962, p. 148 and fig. 52 A) suggests an enlarged foramen. Nothing is known of the infraorbital foramen of *Prolapsus*, but the late Eocene *Protoptychus* was in the early stages of hystricomorphy. There thus is a growing collection of taxa, unfortunately still (except for *Franimys* and *Reithroparamys*) not well known, and probably not members of a single phyletic line, of North American Eocene rodents that show the initial stages of both hystricognathy and hystricomorphy. That is, this assemblage of North American Eocene rodents possessed the necessary potentialities to have given rise to the most primitive of the South American Caviomorpha (although no known genus could have been such an ancestor), and is the only group of Eocene rodents known from anywhere in the world that occupies such a position. As has often been stated, the actual immediate ancestor of the Caviomorpha did not live in the United States, but rather probably in Middle America.

Although I suspect that *Prolapsus* will ultimately be shown to have a distant relationship to the Caviomorpha, I do not believe that any useful purpose would be served by referring it, at present, to the Caviomorpha. It could not have been ancestral, or even approximately ancestral, to the known Caviomorpha, because of its progressive pentalophate cheek tooth pattern, which was developing in a rather unique manner, quite different from the methods followed during Deseadan time by the Caviomorpha. If *Platypittamys*, as seems probable, were primitive in the non-penetration of the infraorbital foramen by the *masseter medialis*, the expansion of this muscle presumably originated within the Caviomorpha after their invasion of South America, and, presumably, followed the development of full hystricognathy. And, if *Platypittamys* were primitive in having four-crested upper and lower cheek teeth (Wood, in press 1), its middle Eocene ancestor presumably did not have teeth as complicated as those of *Prolapsus*.

Hoffstetter (1972, p. 2867) has recently reiterated his contention of special caviomorph-phiomorph relationships, discounting the importance of the discovery of *Prolapsus* in the Eocene of Texas, in spite of the fact that it is the only fully hystricognathous rodent known from the Eocene of the entire world. His insistence on the close similarity of the Caviomorpha and Phiomorpha is reached by ignoring the fact that the Deseadan octodonts (*Platypittamys*) and echimyids (*Deseadomys*, *Sallamys* and *Xylechimys*), the two families that are clearly the most primitive of the caviomorphs, never have cheek teeth (either uppers or lowers) with more than

[8]Michaux (1964) described two species of *Reithroparamys* from the early Eocene of France. Later, he made one species the type of a new genus, *Meldimys*, which he placed in a new European subfamily of paramyids, the Ailuravinae (1968, p. 155), and considered the other species to be generically indeterminate (1968, p. 173). Both species were based on isolated teeth, with no information as to hystricognathy.

four crests. The four crests of the upper teeth quite clearly were the anteroloph, protoloph, metaloph and posteroloph, as may be told by the swellings showing the positions of the paracones and metacones (Wood, 1949, fig. 3 A). In these genera, there is never any suggestion of a fifth crest. As Wood and Patterson pointed out (1959, p. 389-392), the fifth crest (the neoloph) is a new development in the caviomorphs, not homologous to anything in other hystricomorphous rodents (Wood, in press 1).

The assemblage of North American Eocene rodents that includes the Reithroparamyinae, Protoptychidae and *Prolapsus* is also the only known group of Eocene rodents that has the potentiality of having been ancestral to the African phiomorphs. I do not believe that the ancestor of the African forms is to be sought in North America, but rather that hypothetical members of this same broad subhystricomorphous group, that lived in southwestern Asia (Wood, 1972, p. 1251) were the actual ancestors. The most primitive of the early Oligocene phiomyids, *Phiomys andrewsi*, had cheek teeth that seem best interpreted as being in the process of simplification from a five-crested pattern (Wood, 1968, p. 38, figs. 1 C-E, 2 D), which, however, must have been based on the usual rodent method of development of the mesoloph and mesolophid by the transverse elongation of mesocones and mesoconids that arose from the pre-existing mure and ectolophid, respectively, methods of origin quite different from what occurred in *Prolapsus*, where the mure and ectolophid are both absent. The phiomyids, therefore, must have been descended from Eocene ancestors rather different in tooth pattern from *Prolapsus*.

One of the major results of the discovery of *Prolapsus* is that it shows that there is a possible North American ancestry for the Caviomorpha. The absence of known potential ancestors for the Caviomorpha in North America has always been one of the strong supports for the hypothesis of trans-Atlantic rodent migration between Africa and South America. Whatever might have happened in the early Mesozoic, it seems extremely improbable that rodents crossed the South Atlantic around the end of the Eocene, and *Prolapsus* demonstrates the absence of any necessity for such a hypothesis.

Prolapsus sibilatoris,[9] new species
Figs. 5-7

Holotype.—TMM 41372-179, right lower jaw with M_{1-3}, the alveolus of P_4, a broken incisor, and a well preserved angular process.

Hypodigm.—Holotype, eight isolated lower teeth and eleven isolated upper teeth, listed in tables 6 and 7.

Diagnosis.—Large species, with well developed mesoconids and complete or nearly complete hypolophids; complexities prominent in upper cheek teeth, and pseudomesoloph well developed. Measurements as given in tables 6 and 7.

Distribution.—TMM locality 41372, Whistler Squat local fauna, 50 feet above base of Pruett Formation, Big Bend region of Texas.

[9]Genitive of Latin "*sibilator*", a whistler. In reference to Whistler Squat, the locality that furnished the material of this species.

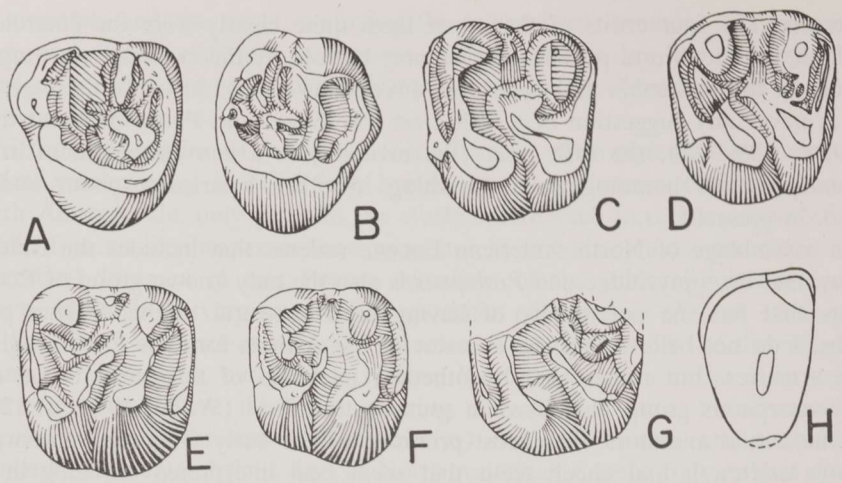

Fig. 7. Upper teeth of *Prolapsus sibilatoris*, new genus, new species, X 10.

A. LP^4, 41372-278. B. RP^4, -297. Anterior end to the right. C. LM^1, -300. D. LM^1, -256. E. RM^1, -285. Anterior end to the right. F. RM^2, -295. Anterior end to the right. G. Broken LM^2, -304. H. Cross section of RI^1, -241G, seen from the front. Antero-mesial corner restored from a short distance along the tooth.

DESCRIPTION

The mesoconids extend at least half way across the lower molars of this species, and always seem to be formed of at least two cusps (fig. 6 C-D, G-J). The hypolophid of M_1 is a complete crest at the wear surface (fig. 6 C-D, G), whereas on M_2 it is slightly interrupted (fig. 6 G). There is often an enlargement of the middle of the hypolophid to form an entoconulid (fig. 6 D, G, H). A crest from the entoconid of M_3 extends into the talonid basin, reaching toward or uniting with the mesoconid, but apparently never reaching the posterior cingulum. A single hypoconulid seems to have been present in the posterolophid. The teeth of the holotype are among the largest known of this species, being exceeded in size only by 41372-284 (table 6).

The pseudomesolophs are well developed and nearly complete in the upper cheek teeth. There is a distinct protostyle at the lingual end of the anterior cingulum of the molars. In most specimens, the metacone reaches the buccal margin of the tooth, but in one (fig. 7 C) there is a continuous cingulum reaching from the mesostylar region to the posterior cingulum.

The features listed above all seem to be advanced characteristics for *P. sibilatoris*, as compared with the smaller and earlier population, described below as *P. junctionis*.

Prolapsus junctionis[10], new species
Fig. 8 A-H

Holotype.—TMM 41444-62, isolated RM_1.

Hypodigm.—Holotype, three isolated upper cheek teeth, six isolated lowers, and one isolated upper incisor, listed in tables 6 and 7.

[10]Genitive of Latin *junctio*, a junction. The material of this species came from two localities, one at and one near the junction of a road and a trail.

Diagnosis.—Smaller than genotype, except for transverse diameters of P_4; mesoconids extend less than half way across lower teeth; hypolophids apparently never complete and entoconids may connect to posterolophid; pseudomesoloph broadly interrupted in center of upper molars; mesostyle small; protostyle not a distinct cusp; measurements as given in tables 6-7.

Distribution.—Basal conglomerate of Pruett Formation, about 50 feet stratigraphically below level of Whistler Squat local fauna; TMM localities 41443 and 41444, Big Bend region of Texas.

DISCUSSION

Comparison was made between the measurements of the sample of teeth of *Prolapsus sibilatoris* and the combined sample from localities 41443 and 41444, here described by *P. junctionis* (omitting 41444-60, probably representing a third and still smaller species), using a modification of a technique described by Simpson, Roe and Lewontin (1960, p. 195-196 and 206-212). It was assumed (table 6) that the means of the sample of *P. sibilatoris* were the actual means of that species ($\overline{X'}$) and that all the cheek tooth measurements of the species had $V = 5$. Comparison with data given elsewhere (Wood, 1962, numerous tables) suggests that this value of V is high for cheek tooth measurements of homogeneous samples of Eocene rodents. These assumptions permit the calculation of an assumed standard deviation (s′) for the *P. sibilatoris* population, which should be as inflated in size as the value of V. On this basis, two measurements (the transverse diameters of P_4) show no difference between *P. sibilatoris* and *P. junctionis*; over half the measurements of *P. junctionis* (14 out of 24) are more than 3 s′ smaller than $\overline{X'}$ of *P. sibilatoris;* and the remainder are smaller, but less than 3 s′ smaller (table 8). It is believed that this consistent size difference, together with morphological differences discussed below, warrants the recognition of *P. junctionis* as a distinct species.

The mesoconids are smaller than in the genotype, although in 41444-59 it is only slightly smaller. The hypolophids are never complete before wear (fig. 8 B-D), and

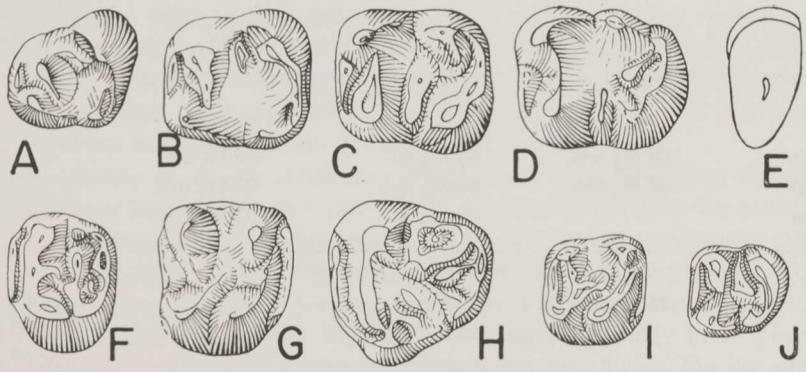

Fig. 8. Teeth of *Prolapsus junctionis*, new species, and of *Prolapsus* sp. indet., X 10.
A-H. *Prolapsus junctionis.* I-J. *Prolapsus* sp. indet.
A. RP_4, 41444-1. B. RM_1, -62, holotype. C. LM_2, -59. D. LM_3, -61, with solution pitting of enamel removed. E. LI^1, -56B, cross section. G. RM^2, -25, anterior end to the right. H. LM^3, 41443-30. I. Rm^1, 41372-279, anterior end to right. J. RM_3, 41444-60.

usually lead backward to the posterolophid rather than being directed toward the hypoconid. In the lower molars, there seem always to be two hypoconulids in the posterolophid. The only intermediate upper molar that is known (fig. 8 G) has a short and simple pseudomesoloph that is widely separated from the mesostyle. The protostyle is basically nonexistent. The pattern of the tooth in general is simple. The upper premolar is more complex and more molariform than are any referred to *P. sibilatoris*. It is the only known element of *P. junctionis* that does not seem to be more primitive than the corresponding element of the genotype.

A third upper molar (41443-30), the only tooth of *Prolapsus* from locality 41443, is larger than the other upper cheek teeth of *P. junctionis* but cannot be compared with M^3 of *P. sibilatoris* as none are known. The anterior half of the tooth shows no features of particular interest (fig. 8 H). A marginal crest runs from the protocone around the rear of the tooth almost to the paracone, and bears five enlargements. The one at the posterior end of the tooth is considered to be the metacone, the two along the buccal margin mesostyles, and the lingual two the posteroloph and the hypocone. A crest curves in toward the center of the tooth, uniting the two mesostyles, and bearing additional complexities. An anteriorly directed ridge from the metacone expands into what is considered to be a metaconule. Another cusplet in the center of the tooth lies between the metaconule and irregular swellings from the protocone and hypocone.

An upper incisor (fig. 8 E) is somewhat different in the shape of the cross section from that referred to *P. sibilatoris*, but agrees with the lower incisors of the genotype in the thick enamel and the comma-shaped pulp cavity, and is of about the correct size to have belonged to *P. junctionis*. The anterior face is not as flat as in the tooth referred to *P. sibilatoris* (fig. 7 H), but this may be related to the smaller size of *P. junctionis*.

TABLE 8

Comparisons between assumed means of cheek tooth measurements of population of *P. sibilatoris* (based on two or more specimens) and individual measurements of specimens of *P. junctionis*.

Teeth of *P. junctionis* from locality 41444 are below assumed means ($\bar{X}'$) of *P. sibilatoris* from locality 41372 by:

Less than 2 s'	2–3 s'	3–4 s'	4–5 s'	over 5 s'
		LOWER TEETH		
-59 M_2 ap	-62 M_1 met	-62 M_1 hyp	-33 M_1 ap	
-61 M_3 met	-59 M_2 met	-65 M_3 ap	-62 M_1 ap	
-59 M_2 hyp	-65 M_3 met	-65 M_3 hyp	-33 M_1 met	
-61 M_3 hyp		-61 M_3 ap	-33 M_1 hyp	
		UPPER TEETH		
	-25 M^2 met	-25 M^2 ap		-26 P^4 ap
		-25 M^2 prot		-26 P^4 prot
				-26 P^4 met

Abbreviations: ap = anteroposterior; hyp = width, hypolophid; met = width metalophid in lower teeth and width, metaloph in uppers; prot = width, protoloph; s' = assumed s; $\bar{X}'$, = assumed mean. For assumed $\bar{X}$ and assumed s, see tables 6-7.

Prolapsus sp. indet.
Fig. 8 I-J

Another and even smaller species of *Prolapsus* is indicated by an RM_3, 41444-60, and an RM^1, 41372-279 (fig. 8 I-J), the former from the junction, the latter from Whistler Squat. These are inadequate for the definition of a species, but they show, besides being much smaller even than *P. junctionis* (tables 6-7) that M_3 has a weak hypolophid, a large mesoconid, and a single hypoconulid, and that M^1 has no mesostyle, an incomplete pseudomesoloph, and a lesser development of minor irregularities on the crown.

AGE OF THE LOWER PRUETT FORMATION AS INDICATED BY THE RODENTS

The assemblage of rodents discussed in this paper seems to be middle Eocene. *Thisbemys plicatus*, from which the Texas specimens cannot be separated, is known only from the early Bridgeran. The late Bridgeran species *T. corrugatus* is appreciably more advanced. *Microparamys minutus* is of general Bridgeran age. The small number of specimens that have been reported do not yet permit differentiating early and late Bridgeran evolutionary stages of *Microparamys minutus*. Several of the specimens discussed as "Paramyidae indet," seem most like (but more advanced than) the early Bridgeran *Paramys huerfanensis*. Another is very similar to an indeterminate form from the middle Eocene of Utah. The various species of *Mysops* that have been described are all Bridgeran, although there is uncertainty as to their distribution within the Bridger Formation (Wilson, 1938, p. 207-216). *M. boskeyi* is, in some ways, more advanced than any of the Wyoming species, but is clearly even more primitive than *Pareumys troxelli* from the early Uintan. The new genus *Prolapsus* is closer to certain Bridgeran sciuravids (lower teeth to *Pauromys*, uppers to *Tillomys*) in tooth pattern than to any other known rodents.

The presence of *Lophiparamys* might be construed as favoring an earlier age, since the genus has hitherto been reported only from the Wasatchian. But it has been an extremely rare genus, occurring along with *Microparamys*, and, like the latter genus, it could well have had a long time range.

The rodents, then, taken either separately or as a group, indicate a middle Eocene age for the basal part of the Pruett Formation. There is much less certainty as to where, within the Bridgeran, the fossils fit, and it would be best, for the moment, to consider the rodent evidence somewhat ambiguous on this point. What evidence there is seems to favor an early Bridgeran age.

There clearly is an age difference between the collection from Whistler Squat and that from localities 41443 and 41444, as demonstrated by the latter being 50 feet lower stratigraphically. *Thisbemys plicatus*, *Microparamys minutus* and *Mysops boskeyi* are present at both levels. There is no detectable evolutionary change in these forms between the two levels, but the last two species are represented by one tooth each at the lower level. The lack of change, especially in *T. plicatus*, suggests a relatively short time interval between the two levels. On the other hand, there does seem to be evolutionary change, at the species level, between *Prolapsus junctionis* of the lower level and *P. sibilatoris* of the higher, apparently due to evolution in place.

There also may be climatic or ecologic differences between the two levels, as

TABLE 9

Composition of rodent faunules from Basal Conglomerate and Whistler Squat

	TMM localities 41443 and 41444		TMM locality 41372	
	No. specimens	%	No. specimens	%
Mysops boskeyi, n. sp.	1	5	49	51
Prolapsus sibilatoris, n. g., n. sp.	–	–	20	21
Prolapsus junctionis, n. sp.	10	48	–	–
Prolapsus, sp. indet.	1	5	1	1
Thisbemys plicatus	6	29	19	20
Microparamys minutus	2	9	2	2
Lophiparamys, sp. indet.	–	–	1	1
Paramyid indet.	1	5	5	5
Total	21	101	97	101

indicated by the changes in the make-up of the rodent fauna (table 9). *Mysops boskeyi* has increased drastically in abundance, correlated with a marked decrease in the frequency of *Prolapsus*; *Thisbemys plicatus* has remained uniformly abundant. The other elements are too rare to have any important bearing on the matter. We do not know the ecological preferences of *Thisbemys*, *Mysops* or *Prolapsus*. *Mysops*, however, was the initial genus of the Cylindrodontidae, a family that, in the Oligocene at least, were burrowers. Although, as suggested above, it perhaps had not yet begun to burrow extensively, it may have had a greater tolerance for aridity or grasslands than did *Prolapsus*. It is possible that the difference in frequency of these forms at the two levels is not due to a change in the ecology, but represents geographic differences, since the localities are about 12 miles apart.

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